

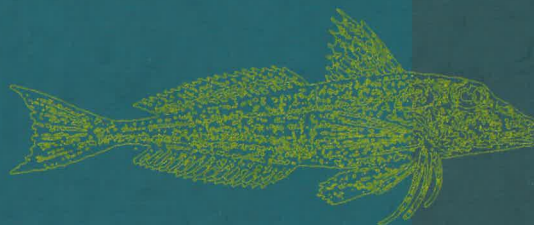
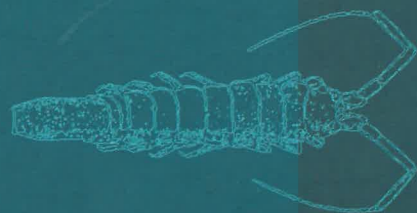
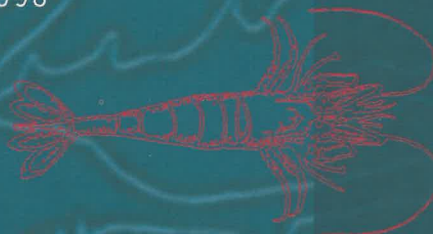
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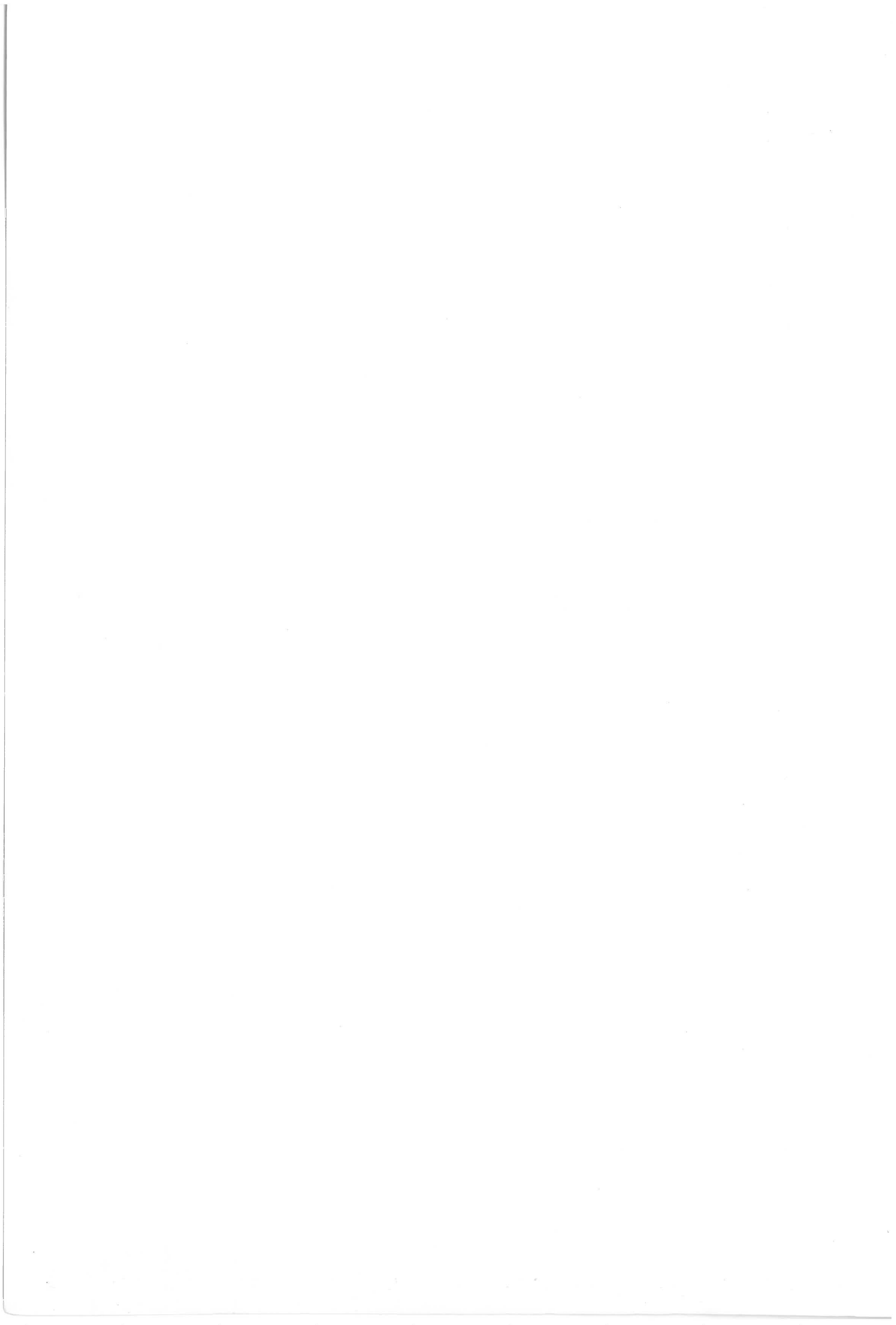
SUSTAINABLE MANAGEMENT OF THE NORTH SEA

ANDRE CATTRIJSSE & MAGDA VINCX

BIODIVERSITY OF THE BENTHOS AND THE AVIFAUNA OF THE BELGIAN COASTAL WATERS

SUMMARY OF DATA COLLECTED BETWEEN 1970 AND 1998





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PREFACE

Since the seventies, Belgian federal research policy aimed at developing scientific expertise to support decision-making linked with the North Sea, in the context of responsibilities at international level. The current 'Sustainable Management of the North Sea' research programme, financed by the Belgian Federal Office for Scientific, Technical and Cultural Affairs (OSTC), covers seven multidisciplinary research projects. Each of these projects aims at supporting a solid scientific background allowing a long-term policy for the use of the resources of the North Sea.

The project 'Structural and Functional Biodiversity of North Sea Ecosystems: Species and their Habitats as Indicators for a Sustainable Development of the Belgian Continental Shelf' investigates the factors that determine and influence the biodiversity of marine ecosystems. The project will translate this information into parameters useful to the policy makers: identification of indicator species, characterisation of sensitive, vulnerable and threatened habitats and setting up criteria for ecological monitoring of the Belgian coastal waters. The subtidal sandbanks so typical for the Southern Bight of the North Sea receive special attention. The project is producing a GIS holding distribution data of the most important benthos and marine bird species and the major habitats occurring in the Belgian waters. The mentioned project also deals with fish parasites and genetic diversity of benthic fish species. The partners in this project are The Marine Biology Section, University of Gent (co-ordinator), the Institute for Nature Conservation of the Flemish State and the Laboratory of Aquatic Ecology of the Catholic University of Leuven.

All data available prior to the start of the OSTC project and knowledge on the structural biodiversity of the benthos and marine birds of the Belgian Continental Shelf are summarised in this review. It includes a full species list of all benthos, marine birds and marine mammals recorded in the study area during the past thirty years. In addition, a complete list of fish parasites recorded in the area is given. The last chapter looks into the genetic diversity of fish in the southern part of the North Sea.

SUMMARY

Marine biologists have intensively studied the Belgian Continental Shelf (BCS) since the early seventies. Still, much of the knowledge on the biology and ecology of the biota collected remains hidden in little accessible and 'grey' literature. A complete overview of all biota, from the plankton to the higher trophic levels, still lacks. This synthesis wants to remedy this by reviewing the knowledge on the biodiversity of the benthos and the avifauna of the BCS.

To detect biodiversity patterns, literature data were collected on diversity measures of the benthos communities. Therefore, the BCS was divided into nine zones. The demarcation of these zones relies partly on geographical and partly on biological information. For each of these zones, data on species number and species richness were collected.

Clear patterns in average species number have been observed for the meiobenthos, the macrobenthos and the hyperbenthos. The species number of benthic assemblages in inshore waters changes dramatically between the eastern and western end of the Belgian coast. A second gradient runs perpendicular to the coastline and involves an increasing species number and diversity offshore. A third gradient relating to depth within a zone needs yet to be confirmed. Also an offshore decrease in density has been observed for macrobenthos and hyperbenthos. Avifauna data do not confirm these patterns even though seabird assemblages offshore differ from the inshore avifauna. All observed patterns need yet to be confirmed by standardised research and monitoring, being the aim of the ongoing programme.

Besides the analysis of structural and functional biodiversity data on benthos and avifauna, this synthesis also examined the knowledge on the genetic structure and the parasite fauna of fish occurring on the BCS. The limited information available on the Belgian coastal waters points at continuity between fish populations of the English Channel, the Southern Bight and the Central North Sea. Genetic differences of fish parasites have been observed in the area and may aid in addressing issues like genetic selection of the heavily fished populations.

1. INTRODUCTION

Belgium holds a long tradition in marine sciences. Since the creation of the smallest North Sea country with the shortest coastline (67km) and a continental shelf of only 3500km², marine scientists have been active in the Belgian coastal waters. It took however more than 140 years before the Belgian authorities decided to fund the marine sciences. In 1970, the first national co-ordinated marine research programme 'Sea' was launched. This programme had, like its successors, an interdisciplinary character and aimed to study the impact of natural and anthropogenic processes on the marine environment.

This synthesis was made for a project that studies the structural and functional biodiversity of benthos, avifauna and selected fish populations of the BCS. The project files within a research programme, funded by the Belgian federal services for science policy, on sustainable development for the Belgian part of the North Sea. The implementation of a GIS based upon benthos and avifauna data is the ultimate goal of this project. For that purpose historic data were brought together and analysed.

The Belgian Continental Shelf (BCS) is the most southwestern part of the Southern Bight of the North Sea and is bordered by the Dover Strait and the Central North Sea. The North Atlantic drift and the freshwater supply of the rivers Schelde and Yzer characterise the watermasses. Strong semi-diurnal tides and a net tidal current, running north-east parallel to the coast, keep the watercolumn well mixed. A gyre, situated in front of the western part of the coast creates a low energy zone. The physical, chemical and biological characteristics of the BCS display a gradient from turbid, nutrient rich and well-mixed inshore waters towards more oceanic transparent and less productive offshore waters. Geologically, the BCS exists of a number of more or less mobile sandbank systems separated by gullies. These subtidal sandbanks possibly may act as 'islands' for the benthos and demersal fauna.

All marine biota have been studied on the BCS but the best-studied components are the plankton and the infauna. The epibenthos has been followed since 1970 but most data have been collected solely for fishery purposes and much information remains unavailable. In the beginning of the nineties the hyperbenthos and the avifauna received attention. Seabird and seamammal countings started back in 1986 but are continued systematically since 1992.

This synthesis summarises scientific information, collected by Belgian scientists since 1970, on the benthos and the avifauna of the BCS, identifying patterns of biodiversity in the area. Despite the fact that many efforts have already

been made to study the biota of the BCS, much information remains hidden in student theses or unpublished reports.

Benthos is here defined as the fauna that is associated with the seabed. The organisms living in the sediments (infauna) are classified as meiobenthos (nematodes and harpacticoids) and macrobenthos (polychaetes, bivalves and amphipods) on a body size criterion. The microbenthos (bacteria and protozoans) has hardly received attention. The organisms living on or nearly on the seabed are called epibenthos. Data collected here include mobile epifauna (decapods, fish, and echinoderms) while data on the sessile fauna were not available. The hyperbenthos comprises all organisms that occur in the lower watercolumn and that live in close association with the sediment (mysids, isopods, amphipods, larval stages of infauna and epibenthos). Furness' (1993) definition was applied to identify the marine avifauna.

Next to the structural biodiversity of the benthos and the avifauna, information on the functional biodiversity of the benthos will be mentioned. Finally, the parasite fauna of fish and the genetic diversity of selected fish populations received attention.

2. METHODOLOGY

To synthesise both the open and the grey literature data, the BCS was divided into nine zones (Fig. 1). The demarcation of these zones is based upon known existing patterns in the benthos on the one hand and on geographical units on the other. The meio- and the macrobenthos communities change along two gradients. Govaere et al. (1980) distinguished three benthic zones in the Southern Bight of the North Sea: a coastal zone, a transition area and the open sea. A second gradual change in the benthos is found in the shallow inshore waters. The negative influence of the polluted waters of the Westerschelde estuary cause the eastern coast to be less species rich than the western end of the Belgian coast. The subtidal sandbanks that are characteristic for the Southern Bight occur in four units on the BCS. We hypothesise that the geomorphology of these sandbank complexes differs such that a distinct benthos fauna is found on them.

Zone 1, the east coast, encloses the shallow inshore waters between the Belgian-Dutch border and the city of Oostende (Fig. 1). Zone 2, the west coast, stretches between Oostende and the Belgian-French border. The northern limit of these two zones was arbitrary chosen as the southern tips of the 'Flemish Banks'. The 'Wenduine bank' is the only sandbank in zone 1 (Fig. 2). The so-called coastal banks the 'Stroombank', the 'Nieuwpoort Bank', the 'Trapegeer', and the 'Smalbank' form Zone 2. The 'Oost Dyck', the 'Buiten Ratel', the 'Kwinte Bank', the 'Middelkerke Bank' and the 'Oostende Bank' constitute the Flemish Banks and form zones 3 and 4. Zone 3 represents the slopes and the tops of these subtidal sandbanks while zone 4 delineates the gullies between them. The -10m LLW line was used to divide between these two zones. The Zeeland Banks form zone 5: the 'Vlakte van de Raan', the 'Akkaert Bank', the 'Goote Bank' and the 'Thornton Bank'. The gullies between these banks are zone 6. Still further offshore lies the Hinder Bank area (the 'Bligh Bank', the 'Oosthinder', the 'Westhinder', the 'Fairy Bank' and the 'Noordhinder'). In analogy with the Flemish and the Zeeland Banks the gullies and the banks form respectively zone 7 and 8. North of the Hinder Banks, the deepest area of the BCS is designated as zone 9 (open sea zone).

For each of the nine zones and for each benthos component and for the avifauna, data on the average number of species per station, diversity indices (Hill's number N_1 and Shannon-Wiener's H') and average density per station were compiled out of the literature and recent unpublished data.

Only the hyperbenthos data allowed comparing diversity indices over the nine zones. For the other benthos fauna data were too scattered or simply too rare for detecting diversity trends over the study area. The only measure for structural diversity that could be used for meio-, macro and epibenthos was the average number of species per station.

Collecting this information produced a benthos species list for the BCS (see appendix). It must be mentioned that this list is far from complete since much information is still unavailable.

FIGURE 1. DESIGNATION OF THE NINE HYPOTHETICAL ZONES ON THE BELGIAN CONTINENTAL SHELF. THE DEFINITION OF THE ZONES WAS BASED ON BIOLOGICAL INFORMATION, ON DEPTH STRATA AND THE GEOGRAPHICALLY SEPARATED SANDBANK SYSTEMS.

— -5m — -10 m — -20 m

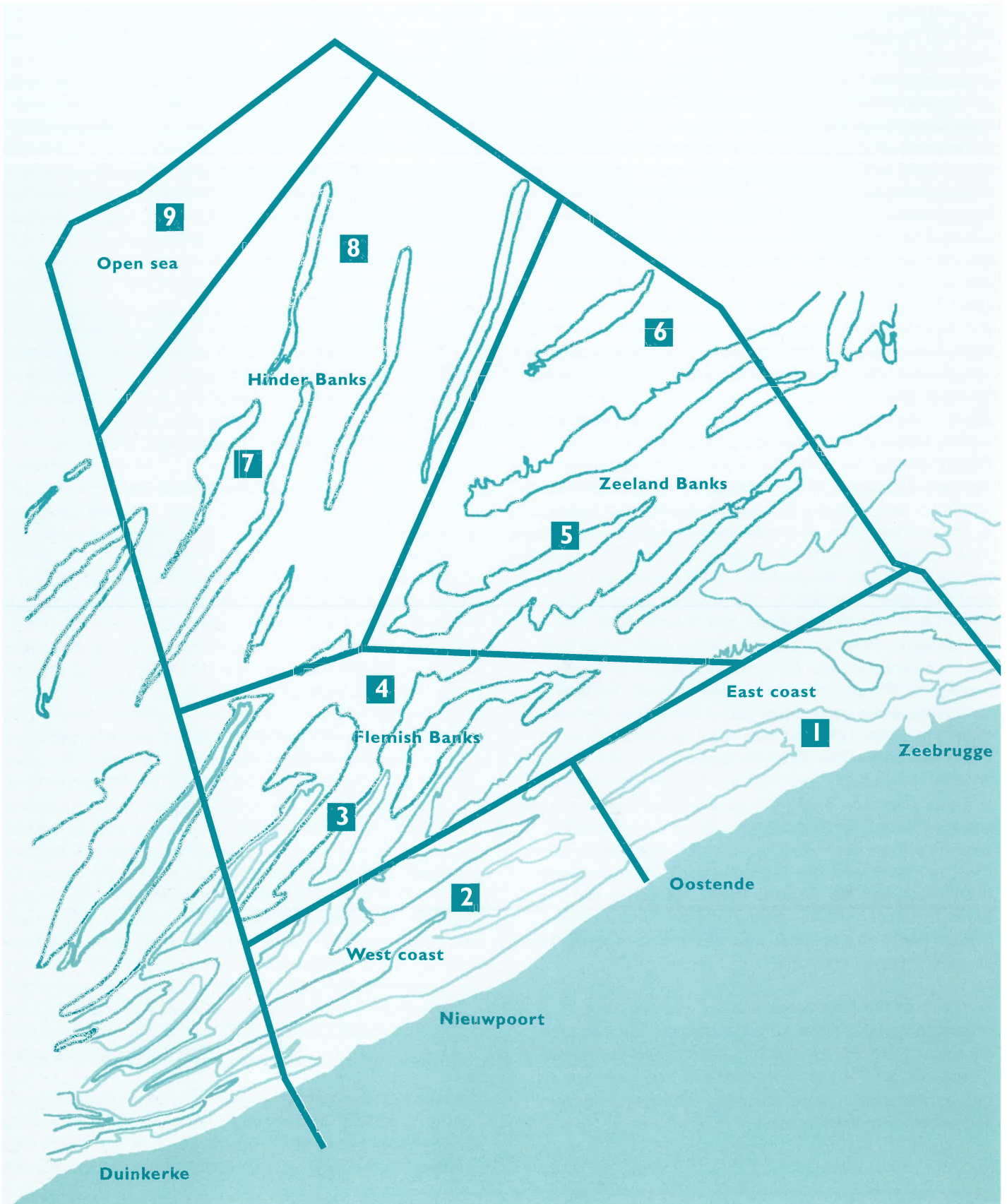
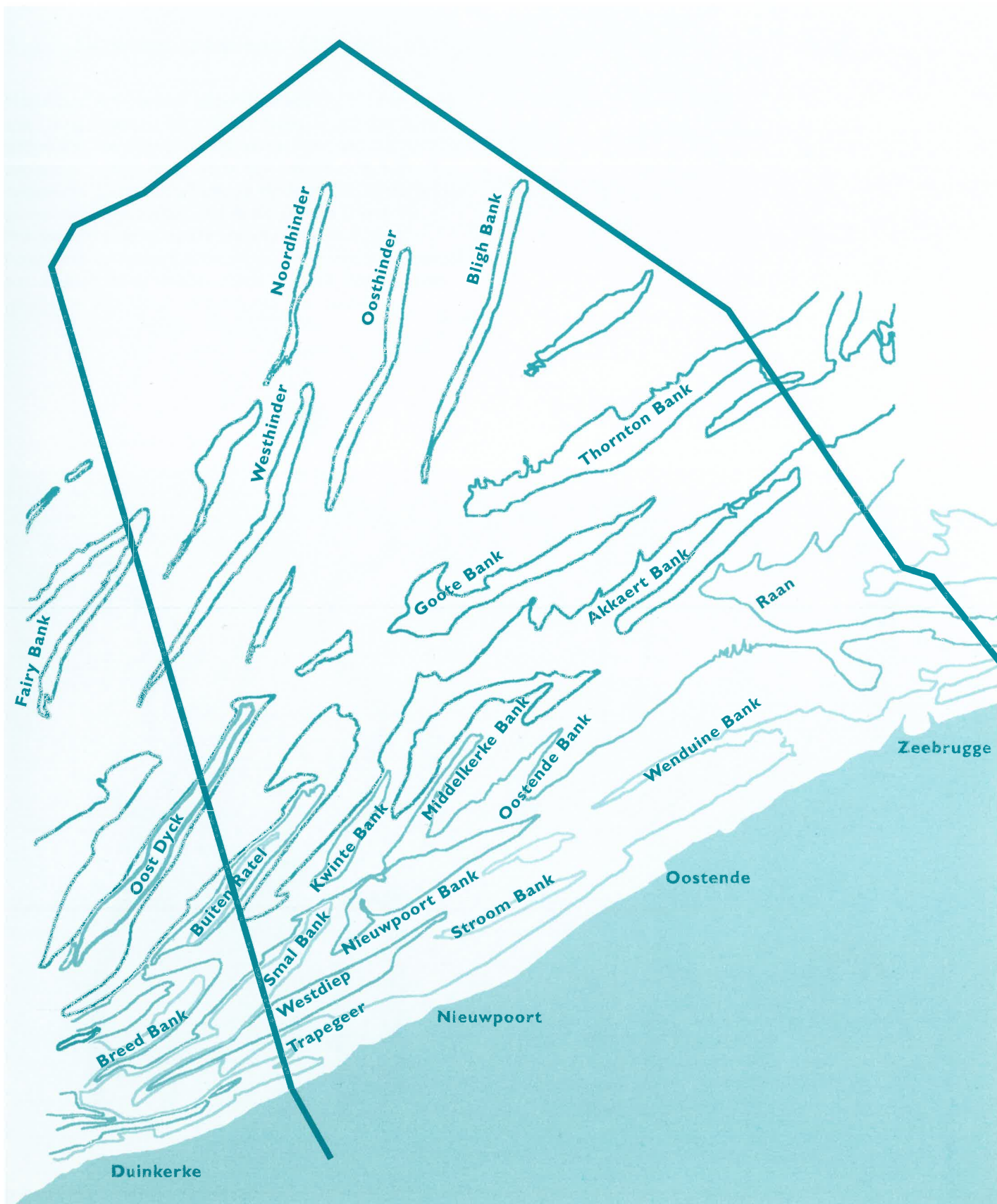


FIGURE 2. THE SUBTIDAL SANDBANKS OF THE BELGIAN CONTINENTAL SHELF.

— -5m — -10 m — -20 m



3. THREE DECADES OF MEIOBENTHOS RESEARCH ON THE BELGIAN CONTINENTAL SHELF: AN OVERVIEW

3.1. INTRODUCTION AND DEFINITION

Meiofauna are benthic organisms passing a 1mm sieve and being retained on a 38µm sieve. Dominant taxa within the meiobenthos are nematodes and harpacticoid copepods, which reach very high densities in soft sediments. Other taxa include kinorhynchs, turbellarians, interstitial polychaetes and many others (Plate 1). Meiobenthos samples are usually collected using boxcorers or reineck boxcorers. These are subsequently subsampled using smaller cores (surface 10cm²), from which the top 10-20 centimetres are studied.

PLATE 1. MEIOFAUNA TAXA

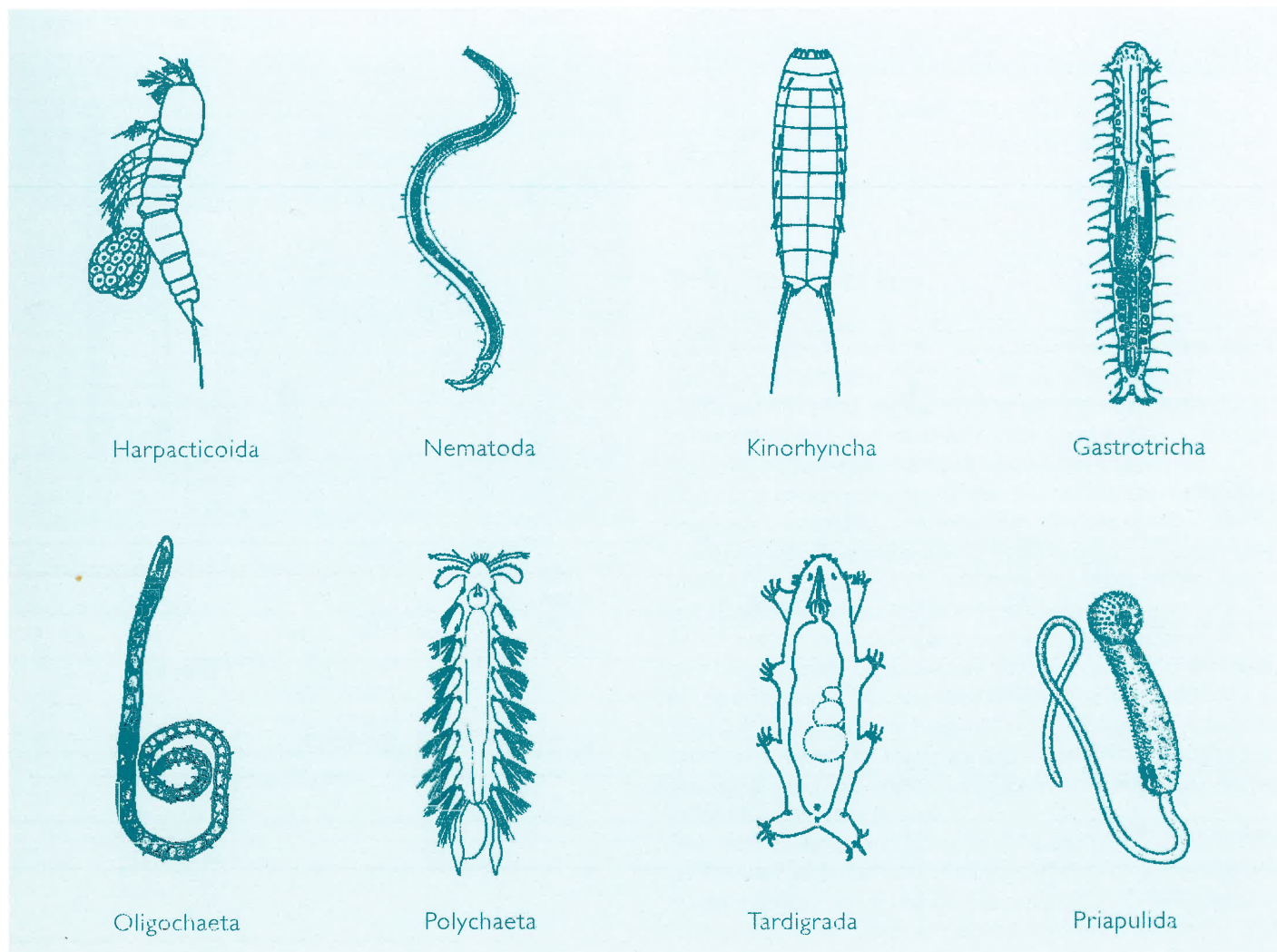


TABLE 1. SUMMARY OF MEIOBENTHOS LITERATURE OF THE BCS. MAXIMUM AND MINIMUM DENSITIES, BIOMASS AND DIVERSITY NUMBERS N_0 AND N_1 ARE GIVEN PER ZONE AND PER TAXONOMIC GROUP. (NEMA = NEMATODES; HARP = HARPACTICOID COPEPODS; TOTAL = TOTAL MEIOBENTHOS)

Reference	Zone	Taxa	Density (ind./10cm ²)	Biomass (gC/m ²)	N_0	N_1
Decraemer 1972	2	nema			2-38	1.12-9.20
Heip & Decraemer 1974	1	nema			13-74	2.33-18.13
Jensen 1974	2	nema			25-31	13.80-18.40
Claeys 1979	3	nema	107-1836	0.083-2.696	21-58	
		harp	34- 577	0.001-0.004	4-18	
Govaere et al. 1980	1-9	harp			0.89/st.(1,2)	1.15 (1,2)
					8.9/st (3)	3.94 (3)
					13.7/st (4-6)	6.63 (4-6)
		total	934-1261(1,2)			
			623-2735(4)			
			757-1640 (5,7)			
Heip et al. 1980	1,2	nema	300-4220(2)	0.290-0.353	4-30	
Heip et al. 1982	1,2,3	nema	2175 (1,2)	0.239 (1,2)		
			628(3)	0.071 (3)		
Willems et al. 1982	3	nema	134-1095		25-54	
		harp	35-342		5-37	
		total	186-1234			
Willems et al. unpubl. report	3	nema	58-1095		25-54	
		harp	25-342		5-37	
		total	186-1234			
Heip et al. 1983	1-9	nema	1190-1920(1,2)	0.160-0.239(1,2)	1-16/st(1,2)	
		harp			13.7/st(3)	6.49(3)
Heip et al. 1984	1,2	nema	706-2472(1)	0.090-0.250(1)	3.8-23.5(1)	
			1337-2285(2)	0.130-0.220(2)	2-11(2)	
		harp	6-45.1(1)		0.005-0.036	10(1)
			1.6-10.8(2)		7(2)	
Heip et al. 1985	1,2	nema	336-2710(1)	0.160-0.239(1)	11-16(1)	
			203-4631(2)	0.189(2)	3-8(2)	
		harp			2-8(1)	
					0-1(2)	
Huys et al. 1986	2	harp			8-20	
Chen 1987	1,2,3,6,9	nema	787(1)	0.149(1)	38(1)	15.83(1)
			1934(2)	0.260(2)	9(2)	4.95(2)
			173-454(3)	0.020-0.028(3)	32-55(3)	7.19-37.76(3)
			639(6)	0.101(6)	55(6)	33.85(6)
			254(9)	0.026(9)	65(9)	40.58(9)
		harp	315(1)		11(1)	2.42(1)
			63(2)		1(2)	1.00(2)
			120-267(3)		9-25(3)	6.20-14.90(3)
			50(6)		12(6)	6.58(6)
			207(9)		33(9)	18.95(9)
		total	1417(1)			
			2318(2)			
			441-806(3)			
			767(6)			
			551(9)			
Vandenberghe 1987	6	nema	358-3781		37-56	
		harp	44-260			
		total	819-4727			
Herman 1989	1,2	nema	706-2758(1)			
			383-4631(2)			
		harp	16.6-121.1(1)	0.010-0.070(1)	1.4-11.95(1)	1.09-2.89(1)
			0.9-121.2(2)	0.001-0.010(2)	1.3-3.8(2)	1.03-1.51
		total	750-2795(1)			
			210-3087(2)			
Vincx 1989	2	nema	55-5610		3-16	
Vincx & Herman 1989	1,2,3,4	nema	948-1509	0.092-0.231		
	6,8,9	harp	20-70	0.004-0.020		
Heip et al. 1990	1-9	nema	1350(1+2)	0.070	5(2)	
		harp		0.008		
Vincx 1990	1,2,3,4	nema			7.6/st(1,2)	3.15-88.00
	6,8,9				30.3(3)	
					22.7(4)	
					32.3-33(6,9)	
Huys et al. 1992	North Sea	harp				5-29
Steyaert et al. 1994	1,2	nema	2528-3268(1)			
			346-1083(2)			
Steyaert et al. 1996	1,2	nema				2.00-7.00(1)
						1.50-6.50(2)

Table 1 shows literature data collected up to present on the BCS. Densities are expressed as ind./10cm². Diversity is expressed as Hill's numbers N₀ and N₁ (Hill 1973). These numbers were calculated from the original data when possible. The Shannon-Wiener diversity index H' was often used in earlier studies, but Heip et al. (1988) preferred the use of Hill's numbers to express benthic diversity. Total biomass values are listed (or recalculated) in gC/m². The C-content of a nematode was assumed to be 0.42*dry weight, the estimated conversion factor for harpacticoid copepods was 0.4*dry weight (C. Neira, pers. comm.).

For some studies, it was not possible to find out which area has been investigated. These studies were therefore not included in Table 1. Some of the listed results not only apply for the BCS but also include data from stations outside the BCS.

3.2. RESULTS

Figure 3 shows that most studies were conducted in the near coastal area. During the history of Belgian meiobenthos research, 68 stations were visited in zone 1 and 58 stations in zone 2. In zone 3, only 10 stations, all on the Kwinte Bank, were investigated while in deeper areas even less research was conducted. No data were found from zone 5 and 7.

NUMBER OF MEIOFAUNA STATIONS PER ZONE

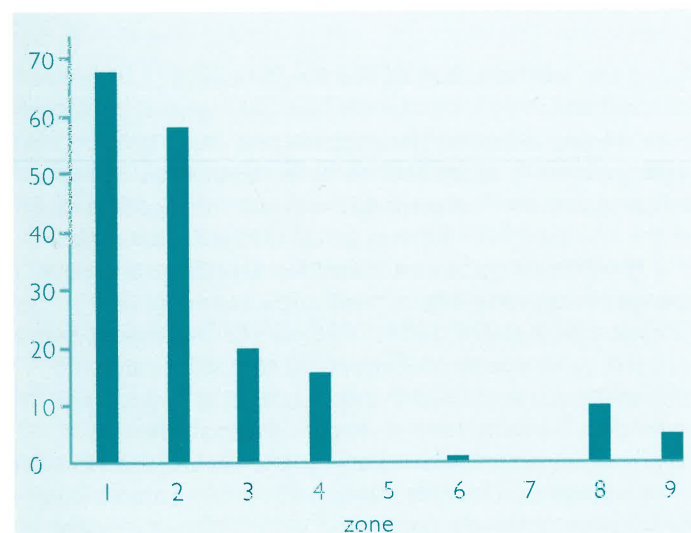


FIGURE 3. INTENSITY OF MEIOBENTHOS STUDIES ON THE BCS.

Mean meiobenthos densities don't differ much and fluctuate between 1000 and 1500 ind./10cm² (Fig. 4). The mean densities on the Kwinte Bank (zone 3) are however much lower.

Despite the absence of any density related trend, a clear pattern in diversity could be found. Diversity within the nematode communities clearly increases with increasing distance from the shore (Fig. 5). A fivefold increase in average species number per station was observed between the inshore and "offshore" zones. The harpacticoid copepod diversity showed a similar pattern (Fig. 6). Here, the data suggest an increase in the mean number of species per station with a factor 30 between zone 1 and 9.

AVERAGE MEIOBENTHOS DENSITY PER ZONE

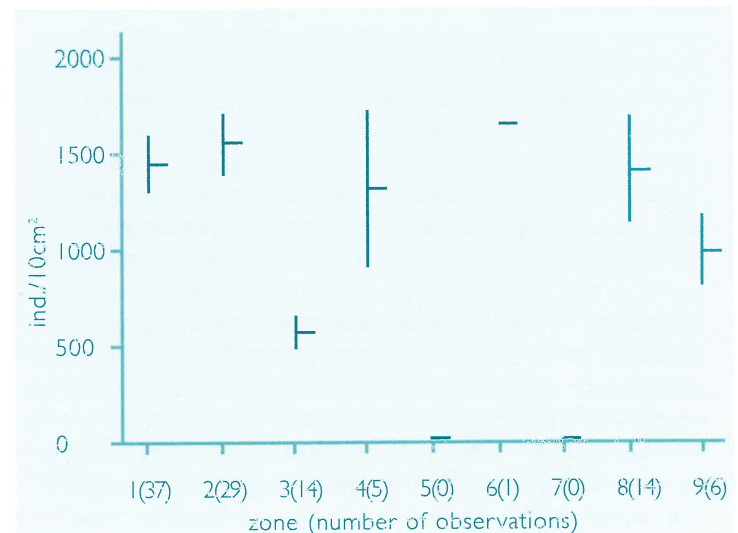


FIGURE 4. AVERAGE MEIOBENTHOS DENSITIES (\pm STANDARD ERROR). THE TOTAL NUMBER OF OBSERVATIONS IS INDICATED BETWEEN BRACKETS.

3.3. DISCUSSION

Care is needed when comparing densities, biomass values and species richness reported by several authors. Different sampling methods (e.g. Van Veen grab, Reineck boxcorer) yield incomparable data (certainly for absolute densities). However, the data used here still allow detecting general trends. Diversity indices are depending upon total sampling size, which in turn depends upon the methodology (sampling equipment, number of stations, number of replicates,...) but form the most objective criterion for comparing different areas.

The increase in species diversity within the nematode and harpacticoid communities from zone 1 to 9 still has to be confirmed by new data originating from stations in zones 4 to 7. Figure 5 suggests that the highest values for nematode diversity are reached in zone 6. In addition, copepod diversity might reach its maximum closer to the coast than in zone 9.

The lack of a pattern in meiofauna density (Fig. 4) should be treated with caution. Mean densities for zone 4, 8 and 9 were mainly collected by Govaere et al. (1980) who used a Van Veen Grab, a method underestimating

meiobenthos density. The absence of a density zonation pattern could further be due to the sampling methodology applied by Willems et al. (1982) for the Kwinte Bank (zone 3). These authors investigated only the sediment down to a depth of 10 cm, while in these kind of well-aerated sediments the fauna can penetrate the sediment down to a depth of 20 cm or more. When comparing their values with cores investigated to 20cm sediment depth, it seemed that they only found 65% of the total fauna.

Based on harpacticoid communities, Van Damme & Heip (1977), followed by Govaere et al. (1980), subdivided the BCS in three zones: a coastal area (< 10 m depth) with a relatively poor community (0.89 species/station, $N_1=1.13$), an open sea community (> 20 m) with a rich community (13.7 species/station, $N_1=6.63$) and a transition zone in between with intermediate values (8.9 species/station, $N_1=3.94$).

Coastal sediments are inhabited by the *Microarthridion littorale*-*Halectinosoma herdmanni*-community. The large surface-dwellers (epibenthic species) and burrowing species (some endobenthic ectinosomatids) of this community are detritus feeders and most common in muddy sands. *Halectinosoma herdmanni*, a large epibenthic species, and *Leptastacus laticaudatus*, a small interstitial species, typify the community occurring in the transition zone. In this area, the organic matter content of the sediments is lower, but stations often contain large amounts of detritus (Heip et al. 1983). The open sea community is characterised by two small interstitial species: the *Leptastacus laticaudatus*-*Paramesochra helgolandica*-community. Since small species dominate, a low biomass is recorded (Huys et al. 1984). Interstitial harpacticoids are grazers, require clean sands and are completely absent in sediments with mud content (Heip 1980). These typical interstitial species of the families Paramesochridae and Cylindropsyllidae form a homogeneous ecological group together with some species of Ectinosomatidae, Diosaccidae and Ameiridae (Heip et al. 1990).

Heip et al. (1984) used both the harpacticoid and nematode community data to subdivide the coastal area in an eastern and a western part, coinciding with the coastal areas used for this synthesis. The eastern area showed less species-rich nematode and copepod communities. Several authors (Herman et al. 1985, Herman 1989, Vincx & Herman 1989) confirmed this. Meiobenthos communities are very well related to the sediment structure. Fine to medium coarse sand dominate the heterogeneous west coast, while at the eastern part the sediment consists of fine to very fine sands with a high mud content. Yet, the copepod community of the coastal zone is not closely associated with sediment characteristics (Heip 1980).

Comparing the nematode diversity of comparable sediments of other European coastal areas, it became clear that the nematode community of the east coast is extremely impoverished. Sediment composition cannot act as the sole responsible factor for this pattern (Vincx & Herman 1989). The high mud content in the east coast sediments originates from the Westerschelde estuary causing a high amount of organic and inorganic pollution (Vincx & Herman 1989). At the muddy stations of the eastern Belgian coastal area, less than five copepod species are found, all being large epibenthic species.

AVERAGE NUMBER OF NEMATODA SPECIES PER ZONE

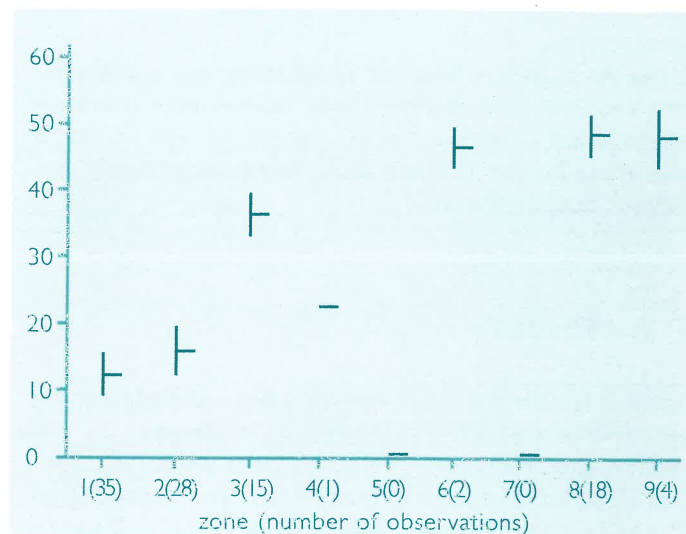


FIGURE 5. AVERAGE NUMBER OF NEMATODE SPECIES PER STATION PER ZONE (\pm STANDARD ERROR). THE TOTAL NUMBER OF OBSERVATIONS IS INDICATED BETWEEN BRACKETS.

Along the western part of the Belgian coast, *Microarthridion littorale* is often the only species recorded from muddy localities. The harpacticoid fauna is also impoverished in sandy sediments on both sides of the Belgian coast and corresponds well with the community of the transition zone (Heip et al. 1990). Recent research in a few coastal stations allowed for assessing long-term changes in the diversity of nematode communities (Steyaert et al. 1994, 1995, 1996, 1999). The overall trend was still valid: coarser sediments, with a wide range of microhabitats, contained more species than finer grained sediments. However, the diversity of nematode communities on a microscale (e.g. the vertical distribution of nematode communities within 10cm²) in an east coast station was positively correlated with the mud content of the sediment. This is due to the higher diversity within non-selective deposit feeders. These species react on an elevated deposition of organic matter associated with fine sediments. This correlation was only established in spring, when oxygen penetrates deeper into the sediment. The relationship disappeared when the sediment turned anaerobic. These findings demonstrate the seasonality of nematode diversity in fine-grained sediments. In contrast, there is a constant high diversity in coarse sediments, since oxygen is always present in the large interstitia. The most surprising result however, was the fact that near the Westerschelde mouth, a shift towards richer nematode communities occurred when compared to the reports written in the eighties (cf. Vincx 1986).

AVERAGE NUMBER OF HARPACTICOIDA SPECIES PER ZONE

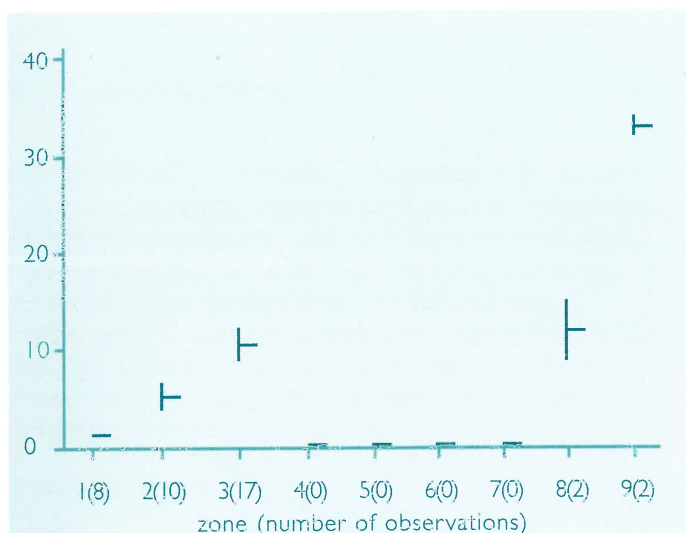


FIGURE 6. AVERAGE NUMBER OF HARPACTICOID SPECIES PER STATION PER ZONE (\pm STANDARD ERROR). THE TOTAL NUMBER OF OBSERVATIONS IS INDICATED BETWEEN BRACKETS.

Vincx et al. (1990) and Vincx (1990) studied the nematode communities of 120 stations in the Southern Bight of the North Sea including both the Belgian and the Dutch Continental Shelf. According to these studies, the BCS should be divided into 5 areas. A coastal area, coinciding with zones 1 and 2, is separated from a transition area, covering zones 4 and 6, which extends onto the Dutch coast. The Kwinte Bank area (zone 3) had a separate community and formed an island within the transition area. Further offshore, 2 areas were distinguished from west to east, the latter one continuing into the deeper coastal waters in front of the Dutch Delta (the Voordelta-area). The coastal area is characterised by a low nematode diversity compared to the other areas ($N_0=7.6$). The nematode community here was dominated by *Ascolaimus* sp.1, *Daptonema tenuispiculum* and *Sabatieria punctata*. In the transition area, 22.7 species/station were counted, with *Enoploides spiculohamatus*, *Paracyatholaimus pentodon*, *Prochromadorella attenuata*, *Richtersia inaequalis* and *Sabatieria celtica* being the most important nematode species, whereas the stations in the offshore area harboured at least 30 species. The western offshore area was characterised by a nematode community dominated by *Ptycholaimellus vincxae*, *Onyx perfectus*, *Rhyps ornata*, *Rhynchonema quemer*, *Spirophorella paradoxa*, *Epsilonematidae* spp. and *Draconematidae* spp., while in the eastern part the most important species were *Chromaspirina parapontica*, *Dichromadora cuccullata*, *Karkinochromadora lorenzi* and *Xyala striata*. On the

Kwinte Bank, situated in the transition area, a mean number of 30.3 species per station was found. The different nematode communities were related to a specific sediment type, however, other environmental variables (e.g. temperature, salinity, chl *a* content, NO_3^- , NH_4^{++}) influenced the distribution of nematode communities as well. The prevailing clean coarse sands in both the open sea area and at the Kwinte Bank explain the high diversity. The high species diversity is reflected in the distribution of the individual nematodes over the four feeding types as defined by Wieser (1953): diversity within feeding types increases when total diversity increases. The coastal area shows a different pattern: low species diversity combined with a loss on trophic diversity. This can partly be explained by the lower habitat heterogeneity (better sorting of the sediments and a high amount of small particles), but it mainly suggests a strong organic pollution in that area.

Within zone 3, only the Kwinte Bank was studied in detail. Claeys (1979) and Willems et al. (1982) give data on the nematode and copepod communities from 10 stations on this sandbank. Harpacticoids are more diverse and more numerous in the coarse sands at the northern end of the sandbank than in the fine sands at the southern end. A total of 65 copepod species were identified.

Vincx et al. (1990) and Vincx (1990) considered the Kwinte Bank as a separate unit on the BCS, characterised by *Bathylaimus parafilicaudatus*, *Desmodora schulzi*, *Leptonemella aphanothecae* and *Onyx perfectus*. A more detailed analysis by Claeys (1979) and Willems et al. (1982) revealed the existence of three different nematode communities on the sandbank. Again, these communities reflect differences in sediment granulometry along the sandbank. Two groups show close similarity, while the third community is characterised by a high relative abundance of the nematode families *Epsilonematidae* and *Draconematidae*. This is exceptional for European 'offshore' nematode communities. Both families are adapted to an instable environment and are mostly found on beaches with strong hydrodynamic regimes. Willems et al. (1982) stated that it should be questioned whether a true sandbank community exists. In such high energetic environments, it could be possible that many species are to be considered as erratic "guests" (Wieser 1959). However, during recent research (Vanaverbeke unpubl.) on the Kwinte Bank, more or less the same nematode communities were found, including the *Epsilonematidae* spp. and the *Draconematidae* spp.. Therefore, the existence of a "Kwinte Bank nematode community", being totally different from the communities in the surrounding areas can be accepted. Claeys (1979) and Willems et al. (1982) used only 100 nematodes from each of 10 stations, originating from 1 sampling campaign. The Kwinte Bank nematode community has consequently not been fully characterised. Chen (1987) studied the nematodes from two stations on the Kwinte Bank and found significant differences in total biomass values between his stations and the ones reported in Claeys (1979) and Willems et al. (1982). Single sampling campaigns are indeed inadequate to gain a complete picture of nematode communities of a highly instable environment.

The harpacticoid copepod communities on the Kwinte Bank show high affinities with the communities from the open sea area. Food input in both systems is low as a consequence of a strong turbulence around the sandbank or of a low input from a nutrient-poor water column in the open sea. Two communities could be discerned on the Kwinte Bank. The first community is typical for coarse sandy sediments, while the other community, including many interstitial harpacticoids is usually found in well-sorted sand. The number of species recorded here is again quite variable: Claeys (1979) reports 4-18 species, Willems et al. (1982) found 5-37 species while Chen (1987) ended up with 9-25 copepod species.

Vincx (1990) found a mean value of 22.7 nematode species per station in zone 4. The channels in between the sandbanks can probably be considered as a transition zone between the species poor coastal area and the more diverse open sea area.

Vandenberghe (1987) studied one station from zone 6. In two replicates, 41 and 52 nematode species were found making the species richness in the channels between the Zeeland Banks comparable with the diversity of the deeper parts of the BCS. This station was situated north of the Thornton Bank at a greater depth than the channel stations in zone 4, explaining the difference in nematode species richness between these two zones.

Little research has been conducted in the offshore parts of the BCS (zone 8 and 9). Only Govaere et al. (1980), Chen (1987), Vandenberghe (1987), Vincx (1990) and Vincx et al. (1990) studied the meiobenthos in these areas. Their data show that the nematode diversity there is higher when compared to the coastal and transition areas. Vandenberghe (1987) recorded 37-56 species in zone 8, whereas Chen (1987) found 55 nematode species in the same area and 93 in zone 9. Chen (1987) also found the harpacticoid communities to be more diverse with increasing depth (12 harpacticoid species in zone 7, 33 species in zone 8). Based on nematode community structure, Vincx et al. (1990) divided the deeper areas in an eastern and western part. Diversity in both areas is however quite similar (east: 32.3 species/station; west: 33 species/station), but a multivariate analysis revealed major differences in the nematode community composition.

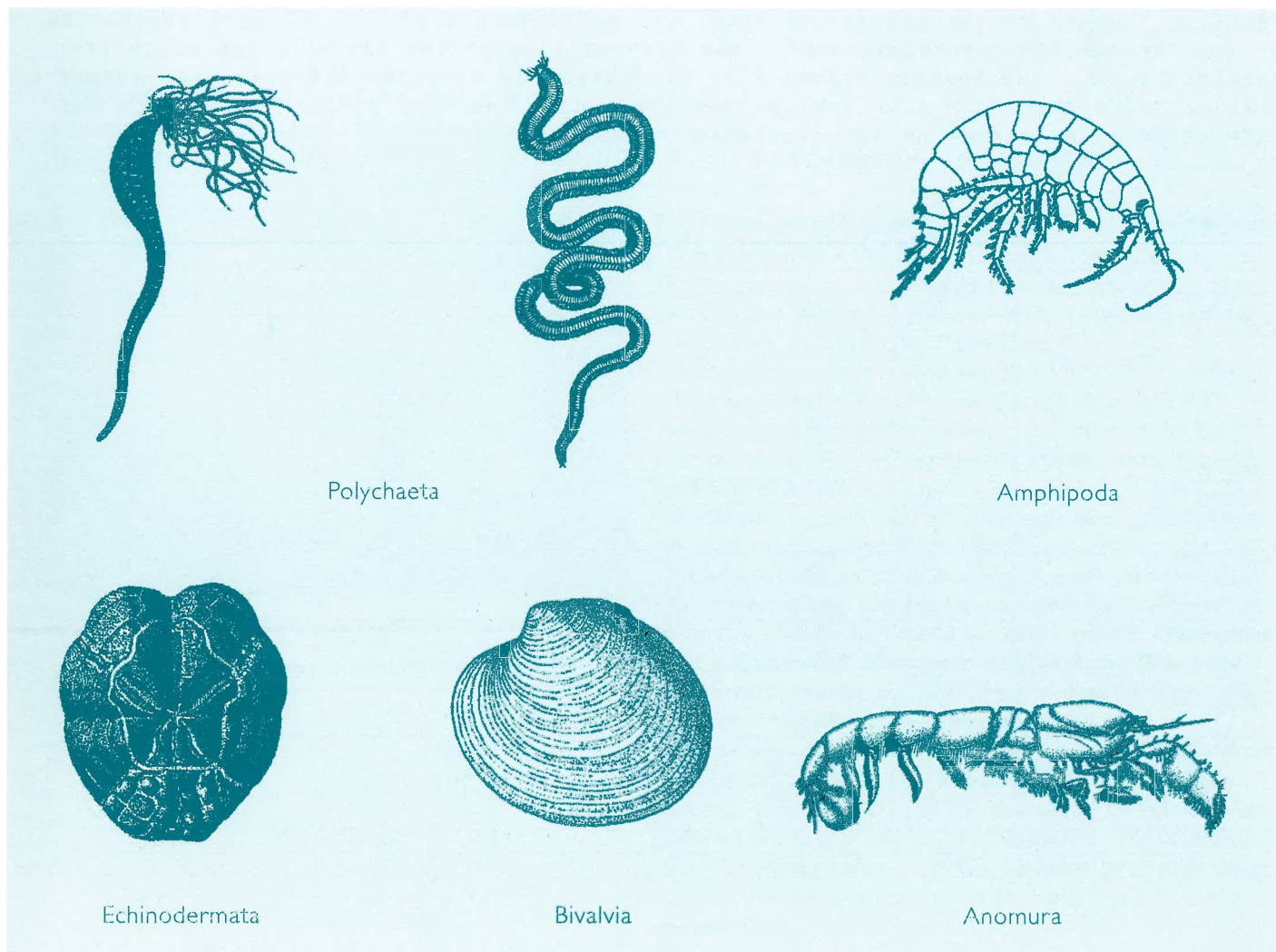
Summarising it can be stated that the BCS can be subdivided into areas with different meiobenthos species richness and community composition. The communities reflect both differences in sediment granulometry and the high organic loading of the sediments near the Westerschelde mouth. Standardised research ought to complete the picture. Temporal variation of the meiobenthos communities has not sufficiently been reported making changes in pollution levels and their effects on benthos difficult to evaluate. The nematode community in front of the Westerschelde estuary has seemingly changed since the beginning of the 1990's, but long-term studies still need to prove this.

4. MACROFAUNA BIODIVERSITY PATTERNS OF THE BELGIAN COASTAL WATERS

4.1. DEFINITION

Macrobenthos is the infauna retained on a 1mm sieve. The most important organisms are bivalves, polychaete worms and amphipods, next to infaunal echinoderms, decapods, gastropods and oligochaetes that are less representative organisms (Plate 2). Burying larger crustaceans like *Callinassa* and some bivalve species like *Ensis* are common in coastal waters but often these animals bury too deep into the sediments for efficient sampling.

PLATE 2. MACROFAUNA TAXA



4.2. RESULTS

Table 2 summarises the macrobenthic literature of the BCS. Like for the meiofauna studies, a number of results apply to the BCS but were based on samples collected on the BCS and/or in the Dutch or French coastal waters. A large methodological discrepancy exists between the different macrobenthos studies. The mesh size of the sieve has changed and concomitantly the moment of sample fixation. The first studies mention the presence of a 250µm sieve under the 0.87mm sieve that allowed to sample smaller size fractions. Only when the published data allowed distinguishing between both size fractions the larger fraction was used in the analysis. It needs mentioning that the results obtained with both methodologies differ substantially and this hampers comparing the data.

The intensity of the macrobenthos research differs strongly between the nine zones. Similar to the meiofauna, the coastal area and the Flemish Banks were far better surveyed than the other regions (Fig. 7). Especially for the gullies between the sandbanks and the most remote open sea area (zone 9) few studies exist.

The recent studies have simultaneously sampled both the slopes of the banks and the gullies between the banks. Zone 6 and 8 have thus been sampled but the data have been presented as data for zone 5 and 7 since it was difficult to track what samples were taken in what stratum. Yet, most samples were collected on the slope of the banks and therefore we consider all samples as slope samples.

Figure 8 represents the average recorded densities for each zone. While the density data for the meiobenthos did not show a trend, the averaged macrofauna densities tend to decrease towards the open sea. The existing methodological differences caution for interpreting these average densities.

The early study of Govaere (1978) covers the whole BCS and contradicts this picture (Table 2). This author describes an increasing average density, average number of species and species diversity (H') towards the open sea. The recent study of Coenjaerts (1997) sampled only four of the nine areas but his results suggest a contrasting pattern: a decreasing density and no trend in inshore-offshore diversity.

Govaere's (1975) data also suggest a more abundant and more diverse macrofauna on the west coast than on the east coast, as pictured in figure 9.

TABLE 2. SUMMARY OF THE LITERATURE ABOUT THE MACROBENTHOS OF THE BCS WITH INDICATION OF THE AVERAGE DENSITY (NUMBERS/M²), THE AVERAGE BIOMASS (MG ADW/M²), THE DIVERSITY INDICES (N_0 , N_1 , AND SHANNON-WEAVER H'), THE NUMBER OF STATIONS PER ZONE, THE NUMBER OF REPLICA TAKEN, THE MESH SIZE (MM) OF THE SIEVE USED AND, THE MOMENT OF FIXATION FOR EACH STUDY (I.E. BEFORE OR AFTER SIEVING OF THE SAMPLE).

Reference	zone	dens (#/m ²)	biom (mg adw/m ²)	N_0 area	N_0 station	N_1	H'	# stations	# replicas	Sieve used	Fixation
Govaere 1975	2	549.0		57	24.1			7	4-5	1	After
Vanosmael 1977	1	4023.3	5597.6	43	15.0		2.01	8	3	0.87	Before
Govaere 1978	1	242.0	1337.0		3.9		1.35	13	2-8	0.87	Before
	2	925.8	2677.5		10.6		2.27	10			
	4	1940.7	4305.8		16.3		2.90	1			
	5	1078.6	1379.4		19.0		3.30	2			
	7	797.5	1078.3		14.2		2.98	2			
	9	4003.6	2935.3		33.0		3.66	1			
Rappé 1978	3	413.1	474.5	53	13.0			10	2	0.87	Before
Van Steen 1978	2	1865.3	10741.8	19	7.6			12	3	0.87	Before
Kerckhof 1980	1	842.2		39	17.0		2.26	3	2-3	0.87	Before
	2	3418.8		57	28.0		2.49	2	2-3	0.87	Before
Meheus 1981	3	1505.0	756.0	34	8.5			6	3	0.87	Before
	3	577.1		45	14.9			10	3	0.87	Before
	5	2171.5	2892.8	29	10.3			4	3	0.87	Before
De Rycke 1982	3	3089.3	1440.5	36	16.7			6	3	0.87	Before
	5	1530.5	2293.8	29	20.3			4	3	0.87	Before
Vanosmael et al. 1982	3	4908.0		73	27.0			10	3	0.87	Before?
Arellano 1995	1	2718.2						2	5	1	Before
	2	1375.2						1	5	1	Before
Coenjaerts 1997	3	1163.0		39	12.0	5.93		42	1	1	After
	4	593.1		54	11.5	6.28		12	1	1	After
	5	835.3		47	10.1	5.73		20	1	1	After
	7	145.4		32	5.5	3.77		21	1	1	After
Philips 1998	3	3009.1		87	19.4	6.46	1.68	103	1	1	After
Degraer et al. 1999a	2			71	5.4	9.80	1.58	40	1	1	After

NUMBER OF MACROBENTHOS STATIONS PER ZONE

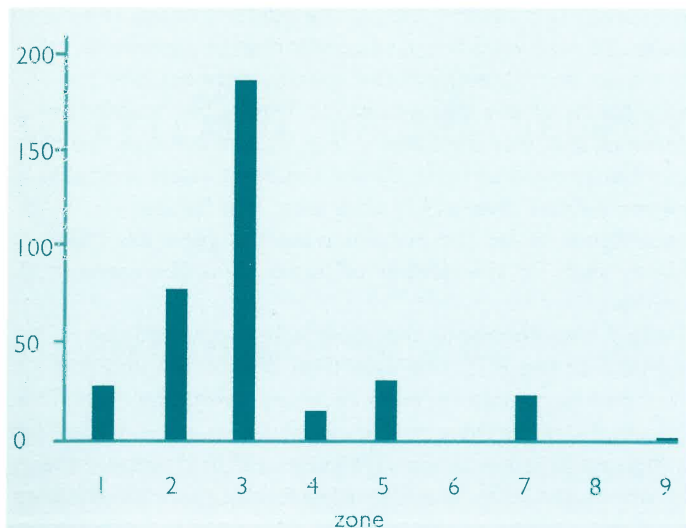


FIGURE 7. MACROBENTHOS RESEARCH INTENSITY ON THE BCS.

In contrast to the results obtained with the meiofauna and the hyperbenthos data (see chapter 5), the average number of recorded species per station for each zone indicates no trend when averaging all studies. Again, the studies of Govaere (1978) and Coenjaerts (1997), the only two studies that sampled over a wide geographical range on the BCS, contradict this.

AVERAGE NUMBER OF MACROBENTHOS SPECIES PER ZONE

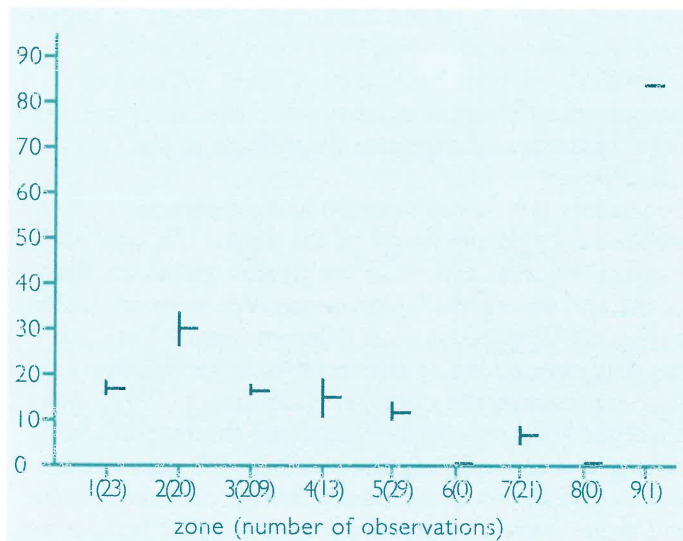


FIGURE 9. AVERAGE NUMBER OF MACROBENTHOS SPECIES (\pm STANDARD ERROR) PER STATION PER ZONE. THE TOTAL NUMBER OF OBSERVATIONS IS INDICATED BETWEEN BRACKETS.

AVERAGE MACROBENTHOS DENSITY PER ZONE

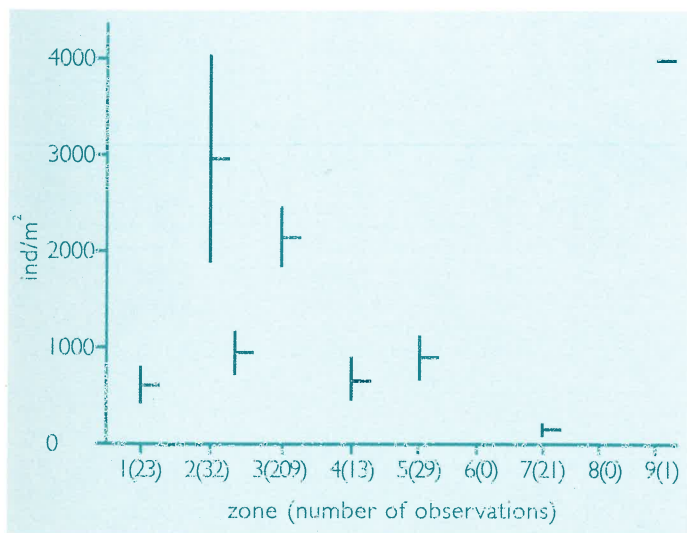


FIGURE 8. AVERAGE MACROFAUNA DENSITY (\pm STANDARD ERROR) FOR EACH OF THE NINE ZONES. THE TOTAL NUMBER OF OBSERVATIONS IS INDICATED BETWEEN BRACKETS.

4.3. DISCUSSION

The sand and gravel mining activities around the Flemish Banks (especially the Kwinte Bank) and the Zeeland Banks and the former industrial waste dumping zone around the Zeeland Banks explain the concentration of macrobenthos studies in these areas.

Reports on the effect of dumping of industrial wastes (titaniumdioxide, thiocarbamate and aniline) on the benthos unfortunately yielded no information on the structural diversity of the benthic communities (Maertens 1984, 1987, 1989).

Vandamme & Heip (77) and Govaere et al. (1980) divided the BCS into three benthic regions: a coastal, a transitional and an open sea region, each with their own communities. The average biomass and the average diversity of the macrofauna increased between the coast and the open sea. Changes in sediment characteristics and organic matter content of the sediments cause the differences in the composition of the benthos communities (Govaere 1975, Govaere et al. 1980, Willems et al. 1982). The inshore-offshore gradient in organic matter content of the sediments correlates well with a parallel gradient in phytoplankton production on the BCS (Govaere et al. 1980). Govaere et al. (1977a) divided the Belgian-Dutch coastal waters in a similar fashion.

Up to date Govaere (1978), Govaere et al. (1977a) and Coenjaerts (1997) are the only studies that covered large parts of the BCS. The contrasting results of both authors can be explained by the sampling methodology. Govaere (1978) used a smaller mesh size and his publication did not allow omitting the smaller size fraction from our analyses. The coarser offshore sediments offer larger interstitial spaces allowing more niches and thus higher species richness. Govaere (1978) indeed reports a fair number of small interstitial polychaete species which could not have been found without the size fraction of 250µm. The total benthic diversity (N_0 per station) likely follows the trend reported by this author but it should be kept in mind that when considering the true macrobenthos organisms only, Coenjaerts' picture might reflect the macrobenthos diversity pattern. Yet, in that study samples were fixed after sieving causing significant loss of individuals.

Coenjaerts (1997) has sampled along transects perpendicular to the length of the banks. This way, each transect includes stations in the deeper gullies, on the slopes and on the shallow bank top. We were unable to distinguish samples taken at different depth strata and this may have added to the result of lower species richness towards the open sea. Coenjaerts (1997) indeed observed a positive relation between the macrofauna density and the diversity and depth. In the gully habitat and on the slopes of the banks coarser sediments occur and richer communities were found. Another feature was that the communities of the north-west side of the bank

differed from those found at the south-east side. The plume of the Westerschelde estuary negatively influences the benthic life on the eastern coast. The deposition of very fine and contaminated sediments by the river decreases both the species richness and the abundance of the macrobenthos. The higher standard error of the average density (Fig. 8) and average species number per station (Fig. 9) for the west coast indicates a higher habitat diversity in that area. The habitat heterogeneity for the inshore waters is generally much higher than for the deeper offshore areas (Govaere et al. 1980).

Table 2 only mentions the studies that covered the subtidal of the BCS. The intertidal of beaches and the surfzone have only recently received some attention. The beach macrobenthos can be divided into a low water and a high water community (De Neve 1996, Mouton 1996, Elliott et al. 1997). The former assemblage bears affinities with the subtidal macrobenthos of the coastal sandbanks (Degraer et al. 1999b). The intertidal position determines the structure of the communities but groins locally disturb the pattern (De Neve 1996).

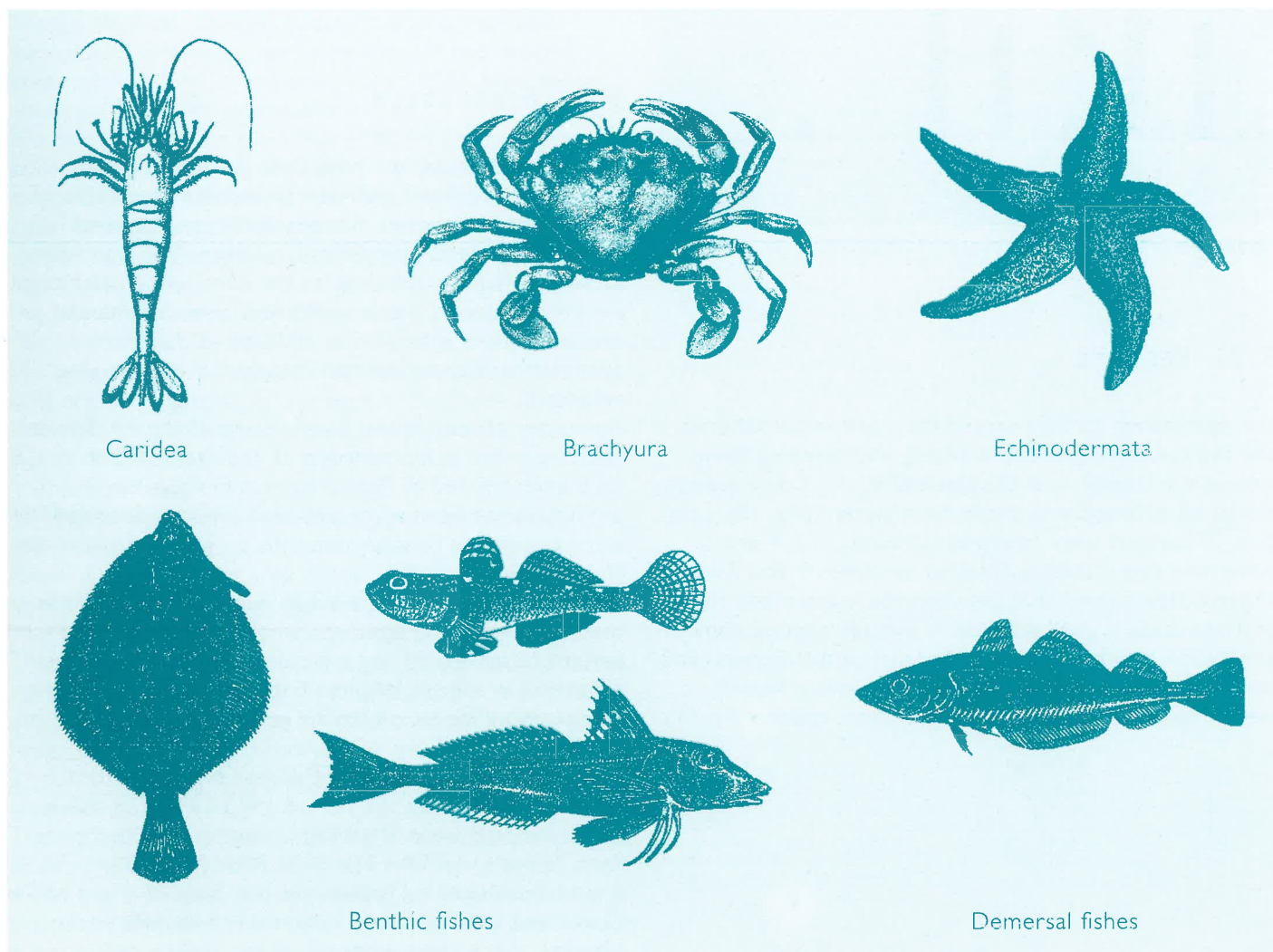
The functional diversity of the macrobenthos has been examined by Govaere et al. (1977b). These authors distinguish a coastal benthic zone with a high productivity and food web of a relative low complexity from an offshore benthic zone with a low productivity and a higher complexity in food web structure. Both zones correspond with the coastal and open sea zones identified by Govaere et al. (1977a, 1980).

5. EPIFAUNA OF THE BELGIAN CONTINENTAL SHELF

5.1. DEFINITION

Epifauna comprises all organisms that occur on or close above the bottom. The working definition for this benthic compartment actually defines epifauna as all organisms caught with a beamtrawl, an ottertrawl or an epibenthic sledge: starfish, sea urchins, squid, shrimp, crabs, benthic and demersal fish (Plate 3). Only relative larger organisms are efficiently sampled since the meshsize of these gears is usually above 5mm. The exclusion of sessile epibenthic organisms like hydroids and bryozooids that cannot be assessed quantitatively further narrows down the term epibenthos for our purpose.

PLATE 3. EPIFAUNA TAXA



Information on the epibenthos of the BCS is extremely scarce and scattered. Except some survey studies of the Fisheries Research Station and the data collected during the beginning of the seventies, no data exist on the distribution of epifauna in the Belgian coastal waters. The latter publications (Redant 1977a, b, Van De Velde & De Clerck 1977) unfortunately do not supply data useful for this analysis. Studies on the ecological monitoring of the epibenthos of the dumping sites do not either (Maertens 1984, 1987, 1989).

The little information available has been extracted from spring and autumn surveys made between 1970 and 1974 (De Clerck & Lybaert 1970, 1971, De Clerck & Cloet 1971a, 1971b, De Clerck & Cloet, 1972, 1973, De Clerck et al. 1973, 1974a, 1974b, De Clerck et al. 1975) of which only the surveys made between 1972-1974 contained data useful for this purpose.

NUMBER OF EPIBENTHOS STATIONS PER ZONE

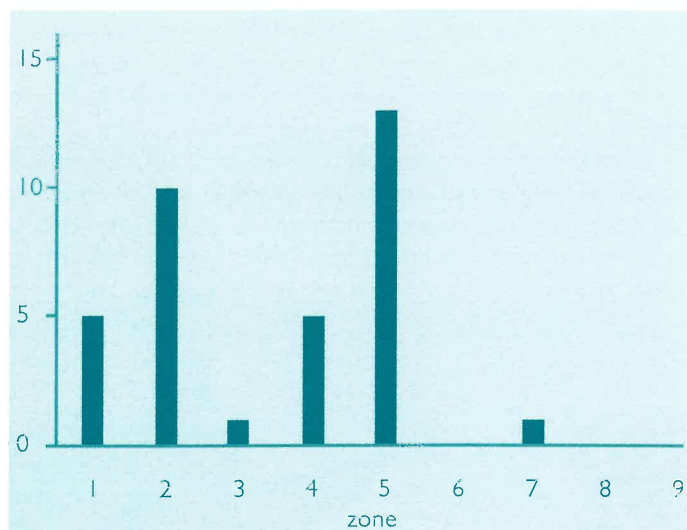


FIGURE 10. EPIBENTHOS RESEARCH INTENSITY.

5.2. RESULTS

The epibenthos surveys served the commercial fisheries and the monitoring of the dredging and dumping zones around the Flemish and the Zeeland Banks. Consequently, almost all data apply to the inshore waters (Fig. 10). Less than 10 stations were followed for zones 1, 2, 4 and 5 while only one station was found for zones 3 and 7. The existing data suggest that between the inshore and the offshore areas a small increase in average species number per station may be present. In parallel with the meio- and macrobenthos, the west coast stations have a higher average species number than the east coast stations (Fig. 11).

AVERAGE NUMBER OF EPIBENTHOS SPECIES PER ZONE

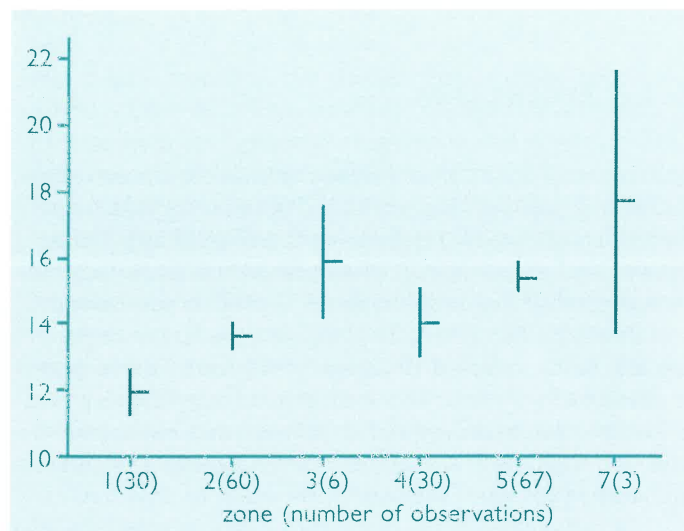


FIGURE 11. AVERAGE NUMBER OF EPIBENTHOS SPECIES PER ZONE (\pm STANDARD ERROR). THE TOTAL NUMBER OF OBSERVATIONS IS INDICATED BETWEEN BRACKETS.

5.3. DISCUSSION

The epibenthos surveys have been made solely for fishery purposes and intended to monitor the stocks of the commercial species. Consequently, the data sets barely allow identifying diversity patterns. The first four surveys only reported data on the commercial species or merely mentioned the occurrence of non-commercial species. From the surveys in 1973 onwards semi-quantitative data on the non-commercial species was recorded.

A number of species that surely occur along the Belgian coast have not been recorded: all four gobies species have been treated as *Pomatoschistus minutus*, no distinction has been made between bib and poor-cod while *Liocarcinus holsatus* refers to six possible swimming crab species.

The possible increase in average number of epibenthos species towards the open sea would agree with the pattern observed for the meio and macrobenthos. The difference in species richness between both ends of the Belgian shoreline exists for the epibenthos as well.

Redant (1977a, b) reviewed the monthly epibenthos surveys made during the period 1973-1975. The three zones sampled were 'Westdiep' (zone 2), 'Vlakte van de Raan' (zone 5) and the Thornton Bank (zone 5). The stations used by Redant are the same of those of De Clerck and colleagues. His results point at differences between these areas. Although there was no difference in average biomass among these areas, some important changes were observed in the biomass composition of

both the invertebrates and the fish. While around the Thornton Bank starfish and brittle stars dominated the communities, shrimp and swimming crabs were more abundant in the area of the 'Vlakte van de Raan' where echinoderms constituted only a small fraction of the total biomass. The echinoderms were only completely absent in the 'Westdiep' in the western coastal zone.

The biomass composition of the demersal and the epibenthic fishfauna of the three areas differed similarly in dominance. The differences between the Thornton Bank and the other two areas were mainly due to the occurrence of bib at the Thornton Bank. Dragonet and gobies dominated the catches in the Westdiep. Dragonet being only abundant in this area (Redant 1977b).

Data on the occurrence of fish eggs and larvae between 1972 and 1975 have been given by Van De Velde & De Clerck (1977). The west coast was characterised by a higher diversity of fish larvae and a higher number of species than east coast, the 'Raan' or the Thornton Bank.

Maertens (1984) summarises the monitoring data of the epibenthos of seven stations, sampled between 1977 and 1981. Four of these lie in the deeper zones around the Zeeland Banks (zone 6), the others are inshore stations on the east coast. Maertens (1984) observed clear differences in the epibenthic communities between both zones. Lower densities, lower biomass and lower diversity occurred in the coastal zone. Densities and biomass of coastal stations were strongly influenced by dredging and dredge disposal activities. Seastars, brittle stars and gadoid fish dominated the epibenthos of the deeper areas while shrimp, crabs and young flatfish were more abundant in the inshore stations.

In a later publication Maertens (1987) compares the epifauna of monitoring stations of industrial waste disposal sites in the area of the Bligh Bank and Thornton Bank (zone 8, 3 stations) and stations of the coastal zone (zone 1 and 2, 7 stations). In contrast to the previous report, the author now found much lower densities in the offshore stations. The differences in faunal composition remain however: shrimp and crabs dominate the inshore epibenthos while echinoderms dominate the offshore communities. In this report, Maertens (1987) also observed a clear difference in the inshore epifauna densities: total densities at the west coast are higher than at the east coast.

The lower densities offshore was again confirmed by Martens (1989). Ten years of monitoring proofed the lower densities in the area of the Hinder Banks. This series of data also showed that the epibenthos hadn't changed substantially during that era.

These studies let us assume that the zones defined in the introduction likely exist for the epifauna: the west coast differs from the east in terms of abundance, offshore lower densities seem to occur and, the epifauna of the Zeeland Banks differs from the epifauna in the inshore waters.

The epifaunal foodchain of the Belgian coastal waters was drawn by Redant (1977b,c) in which brown shrimp, swimming crabs and gobies play a most important role as predators and prey. The role of brown shrimp as essential fooditem for the fishfauna was described by this author in detail (Redant 1980a,b, 1982a,b). The trophic position of gobies has also been studied in detail by Hamerlynck and co-authors (see references).

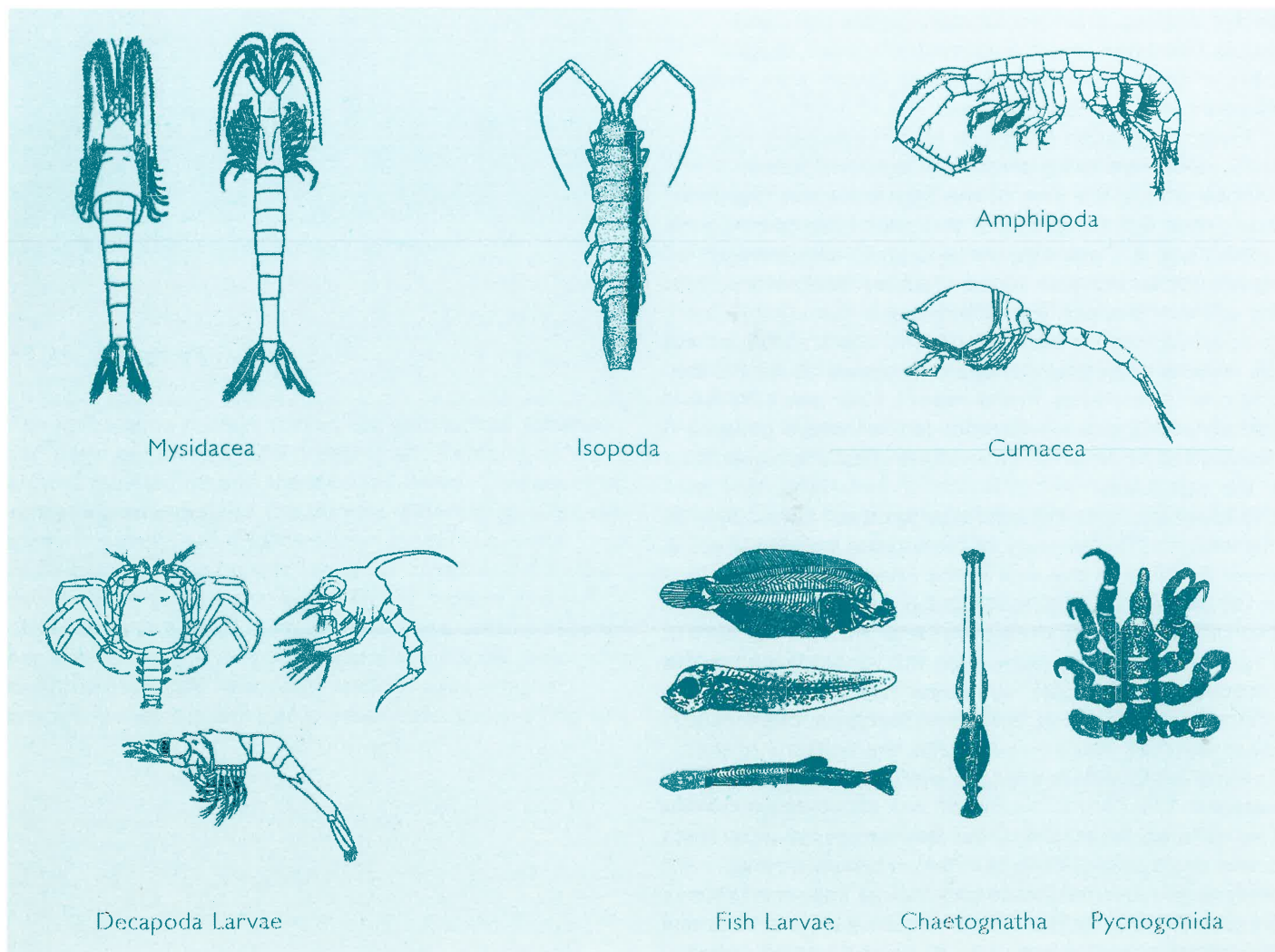
6. HYPERBENTHIC BIODIVERSITY PATTERNS OF THE BELGIAN COASTAL WATERS

6.1. INTRODUCTION AND DEFINITION

The hyperbenthos are the organisms (vertebrates and invertebrates) occurring in the lower meter of the watercolumn, living in close relation with the bottom and being larger than 1mm (Mees & Jones 1997). This fauna has two components: a permanent one consisting mainly of mysids, amphipods and isopods and a temporal/seasonal one which mainly include eggs and larvae of macrobenthic and epibenthic organisms (Mees & Jones 1997).

The hyperbenthos is generally being sampled with a sledge. The definition is a working definition, which actually does not distinguish the epibenthos strictly from the hyperbenthos. Hyperbenthos organisms are too small to be efficiently caught with the standard epibenthos sampling gear. Hyperbenthic sledges usually contain nets with a too small mesh size to sample epibenthic organisms in a representative way.

PLATE 4. HYPERFAUNA TAXA.



6.2. RESULTS

Today only one study paid attention to the hyperbenthos of the BCS and these data are still unpublished. Figure 12 shows the distribution of the sampling stations over the nine zones. In contrast with the studies of the other benthos fauna there is a more or less even spread of stations over the whole BCS.

The average density is highest in the coastal zone and decreases towards the open sea (Fig. 13). The variability also clearly decreases along the same axis.

NUMBER OF HYPERBENTHOS STATIONS PER ZONE

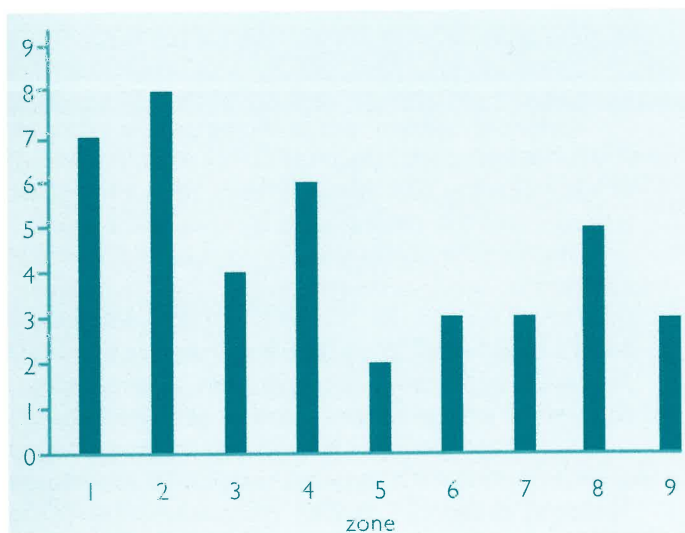


FIGURE 12. INTENSITY OF HYPERBENTHOS RESEARCH.

AVERAGE HYPERBENTHOS DENSITY PER ZONE

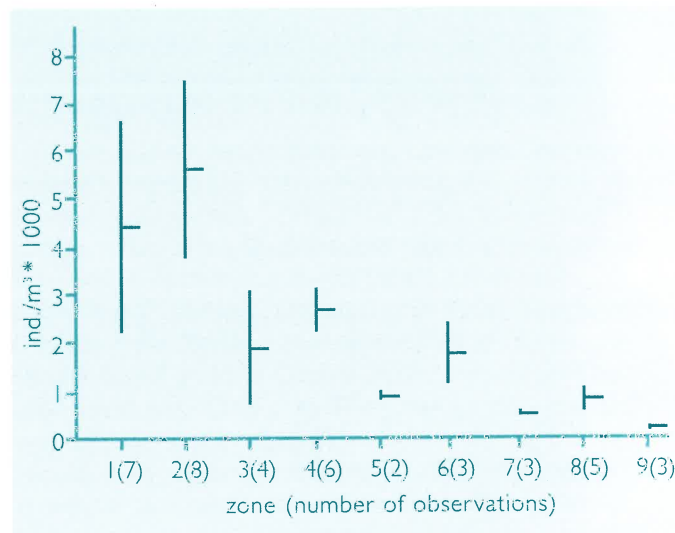


FIGURE 13. AVERAGE DENSITY OF HYPERBENTHOS (\pm STANDARD ERROR) PER STATION PER ZONE. THE TOTAL NUMBER OF OBSERVATIONS IS INDICATED BETWEEN BRACKETS.

The average number of species per station is similar all over the BCS, except for zone 1 and 9 where a lower species number has been recorded (Fig. 14). The habitat of the gullies between the Zeeland and the Hinder Banks, zones 6 and 8, are clearly much richer than the habitat of the banks. This difference was not observed for the Flemish Banks.

Diversity, expressed as N_1 , increases with distance from the coast. At the impoverished east coast, the lower number of species per station results in an extremely low diversity. The open sea habitat is however very rich (Fig. 15). Again, the gradients in structural diversity (east coast-west coast, inshore-offshore and gully-slope) shown by other benthos components exist for the hyperbenthos as well. The east coast harbours both in quantitative and qualitative terms, poorer assemblages than the west coast. The average density (Fig. 13), the average number of species per station N_0 (Fig. 14) and the diversity N_1 (Fig. 15) are lower in the former area. Average density is higher inshore than offshore but the average diversity shows an opposite picture. In addition, a depth gradient was observed: the gullies being more diverse than the slopes of the sandbanks.

6.3. DISCUSSION

The hyperbenthos studies of the BCS are very recent and no data have been published so far, except from Dewicke & Mees (1996) who describe the communities in short. Community analyses of the hyperbenthic fauna of the BCS (Dewicke & Mees 1996) show a very similar pattern as given for meio- and macrobenthos by Govaere et al. (1980). Two species poor communities with high densities occur inshore. The spatial distributions of these two communities coincide with zones 1 and 2. North of these, in the area of the Flemish Banks and the Zeeland Banks a third community was identified which had an intermediate density and a high diversity. The fourth community, found around the Hinder Bank area and the most northern part of the BCS, was characterised by the lowest density and the highest diversity (Dewicke & Mees 1996).

AVERAGE NUMBER OF HYPERBENTHOS SPECIES
PER ZONE

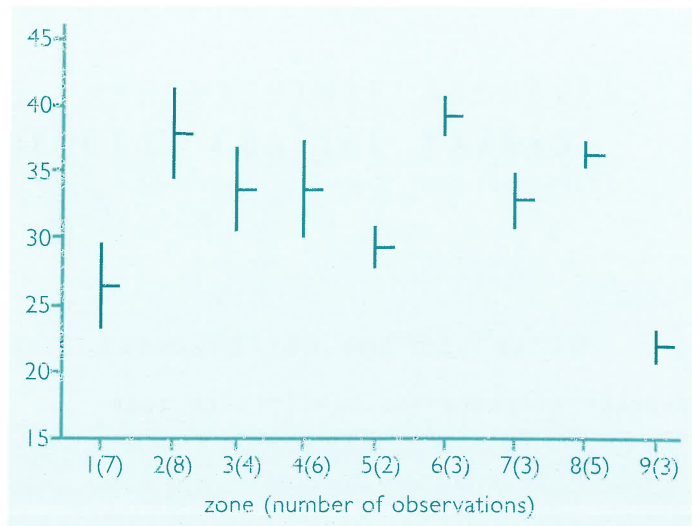


FIGURE 14. AVERAGE NUMBER OF HYPERBENTHOS SPECIES (\pm STANDARD ERROR) PER STATION PER ZONE. THE TOTAL NUMBER OF OBSERVATIONS IS INDICATED BETWEEN BRACKETS.

AVERAGE HYPERBENTHOS DIVERSITY PER ZONE

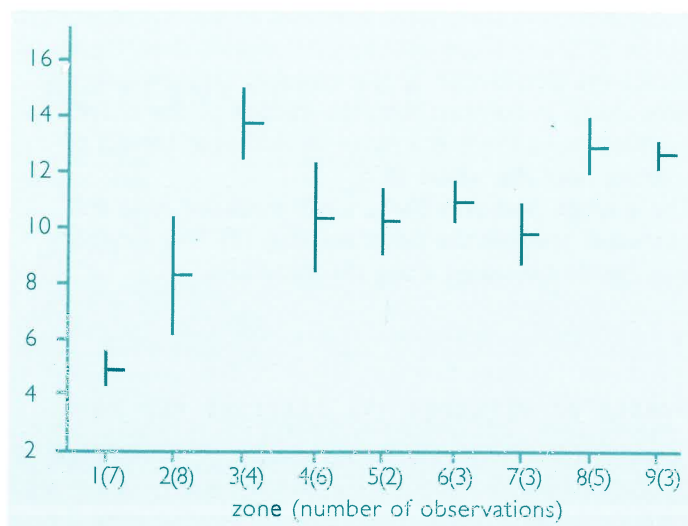


FIGURE 15. AVERAGE DIVERSITY OF THE HYPERBENTHOS, EXPRESSED AS HILL'S NUMBER N_1 , FOR EACH ZONE. THE TOTAL NUMBER OF OBSERVATIONS IS INDICATED BETWEEN BRACKETS.

7. THE BELGIAN MARINE AVIFAUNA

7.1. INTRODUCTION AND DEFINITION

The lack of information on the distribution of seabirds within the Belgian maritime waters and the observation of mass strandings of oiled birds in the eighties (with a peak in 1990) were the main triggers to set up a seabird monitoring programme at the Institute of Nature Conservation in 1992. Although counts of seaducks from aeroplanes were already carried out systematically since 1986, the first ship-based counts by the Institute of Nature Conservation (IN) - necessary to obtain information about other seabird species - commenced in September 1992.

Using the standardised method of Tasker et al. (1984) regular surveys were organised with research vessels ('Belgica' and 'Ter Streep') and ferries, the latter in order to get a proper idea of temporal patterns in the occurrence of seabirds between Oostende and the ports of Dover/Ramsgate, the former in order to produce distribution maps and estimate population strengths of the different species.

For the analysis of bird biodiversity, data of Dutch and British birdwatchers collected before 1992 during accidental expeditions within the Belgian maritime waters, were added to the database of the IN. All observed bird species are identified at sea. This includes both the seabirds *sensu strictu* and the high number of migrants occasionally found within the study area and not directly dependent on marine ecosystems. Divers, grebes, petrels, cormorants, skuas, gulls, terns, auks, seaducks, eider *Somateria mollissima* and long-tailed duck *Clangula hyemalis* are considered as the true seabirds (Furness, 1993).

Additional information on this subject is available from a few overview articles/reports, dealing with surveys within and nearby the study area (Blake et al. 1984, Offringa et al. 1996, Tasker et al. 1987, Camphuysen & Leopold 1994). Other publications refer either only to a smaller part of the study area (Joiris 1976), are incomplete (Boer 1971; Joiris 1972), or are restricted to certain seabird species (Maertens et al. 1988, 1990, Offringa & Meire. 1995).

7.2. RESULTS AND DISCUSSION

The Channel doormat (defined here as the rectangle: 51°-52° N - 1°-4° 30' E) including the Belgian Continental Shelf is of international importance (> 1% of biogeographical population of species) for small divers *Gavia stellata/arctica*, Great-crested Grebe *Podiceps cristatus*, Gannet *Morus bassanus*, Common Scoter *Melanitta nigra*, Little Gull *Larus minutus*, Common Gull *L. canus*, Lesser Black-backed Gull *L. fuscus*, Herring Gull *L. argentatus*, Great Black-backed Gull *L. marinus*, Common Tern *Sterna hirundo*, Sandwich Tern *S. sandvicensis* and Little Tern *S. albifrons* (Offringa et al. 1996). The Voordelta (including the Zeeland Banks), the Flemish Banks, the Hinder Banks and the Coastal Banks are key sites for bird protection within this area. The Channel doormat attracts large numbers of *Larus*-gulls and terns during the nesting period, is an important feeding area for migrating Gannets in autumn and holds internationally important winter concentrations of Great-crested Grebes and Common Scoters. Large flocks of *Larus*-gulls, Fulmars *Fulmarus glacialis* and Kittiwake *Rissa tridactyla* are attracted as scavengers to fishing vessels providing them with discards, offal and unmarketable fish. Hence, their distribution is primarily determined by the presence of a Dutch, Belgian and French fishing fleet. Gannets and Great Black-backed Gulls are more pelagic birds and their highest densities are found in the Deep Water Channel. Diving, self-fishing birds such as auks, divers and grebes concentrate on the Flemish, Hinder, Zeeland and Coastal Banks, where they find their favourite prey on the slopes or in between the banks. The Little Gull occurs in very important numbers in all seasons except summer, and it is estimated that probably almost the entire biogeographical population (70.000 ind.) visits the Belgian Continental Shelf every year. It is suggested that the BCS acts as a 'stepping stone' for birds wintering in the Channel or more to the south, nesting at the North Sea coasts or more northwards. (divers, Gannet, Great Skua *Stercorarius skua*, Little Gull, Lesser Black-backed Gull and Razorbill *Alca torda*). For Great Black-backed Gulls, Fulmars and Guillemots *Uria aalge* of the North Sea, the Channel doormat constitutes the most southern stronghold of their distribution.

For further analysis, only data of seabirds *sensu strictu* will be used. This prevents a bias towards higher diversity in coastal areas, since more small songbirds, waders, etc. are being observed here. Data are presented per season with: winter = December-February, spring = March-May; summer = June-August and autumn = September-November.

Counting efforts show marked differences between regions and seasons. Most data were collected during winter and autumn, efforts in summer are minimal due to a reduction in the availability of vessels. Important data gaps on the Hinder Banks in this season are the result and should be kept in mind when interpreting the data. Likewise, throughout the year efforts are minimal for the most northern and eastern part of the BCS (Fig. 16).

Common Scoter, Herring Gull and Lesser Black-backed Gull are numerically the most abundant species on the BCS and were observed > 50.000 times between 1982-1997. Species observed 10.000-50.000 times, considered as common birds are Kittiwake, Great Black-backed Gull, Common Gull, Black-headed Gull *Larus ridibundus*, Gannet and Guillemot. Regular species, observed at least 1.000 times, include Little Gull, Eider, Fulmar, Great-crested Grebe, Razorbill, Common Tern, Sandwich Tern and

FIGURE 16. COVERAGE OF THE BCS PER SEASON, USING THE STANDARD SEABIRD COUNTING METHOD, FOR THE PERIOD 1982-1997. SYMBOLS REPRESENT COUNTING EFFORT, EXPRESSED AS TOTAL AREA COVERED (KM²) PER 1'x 1' GRID.



Red-throated Diver. Uncommon species are Cormorant *Phalacrocorax carbo*, Great Skua, Velvet Scoter *Melanitta fusca*, Arctic Skua *Stercorarius parasiticus*, Puffin *Fratercula arctica* and Arctic Tern *Sterna paradisaea* (100-1.000 individuals). Rare species, observed less than 100 times, are Black-throated Diver *Gavia arctica*, Manx Shearwater *Puffinus puffinus*, Yellow-legged Gull *Larus cachinnans*, Mediterranean Gull *L. melanocephalus*, Pomarine Skua *Stercorarius pomarinus*, Long-tailed Skua *S. longicaudus*, Leach's Petrel *Oceanodroma leucorhoa*, Storm Petrel *Hydrobates pelagicus*, Red-necked Grebe *Podiceps griseigena*, Black Tern *Chlidonias niger*, Long-tailed Duck and Little Auk *Alle alle*. Very rare species that are observed less than 5 times during the ship-based surveys, are Little Tern (although breeding in the harbour of Zeebrugge in substantial numbers), Northern Great Diver *Gavia immer*, Sabine's Gull *Larus sabini*, Glaucous Gull *L. hyperboreus*, Ring-billed Gull *L. delawarensis*, Gull-billed Tern *Gelochelidon nilotica*, Black-necked Grebe *Podiceps nigricollis*, Great Shearwater *Puffinus gravis* and Sooty Shearwater *P. griseus*.

AVERAGE NUMBER OF SEABIRD SPECIES PER ZONE

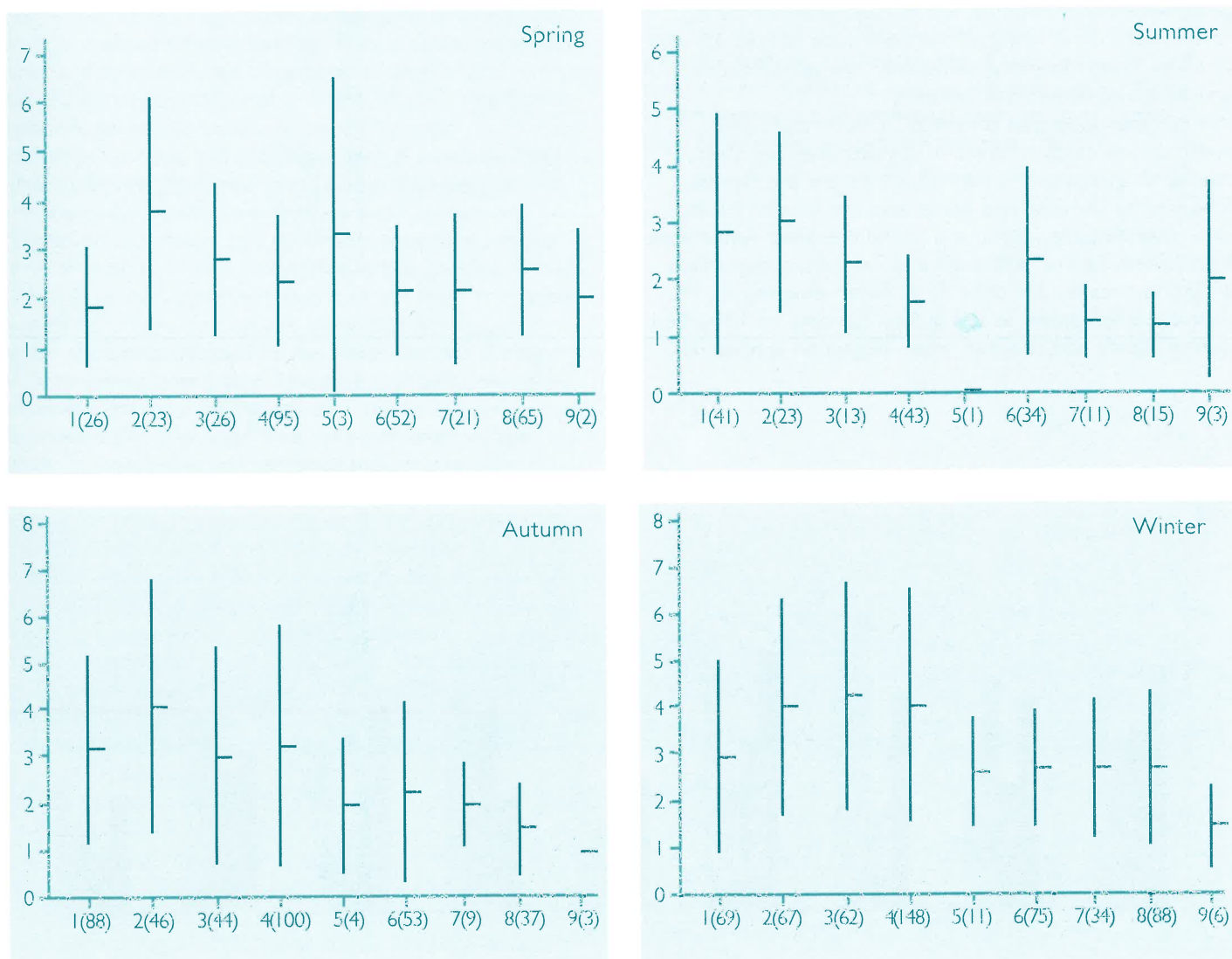


FIGURE 17. AVERAGE NUMBER OF SEABIRD SPECIES PER ZONE (\pm STANDARD ERROR). THE NUMBER OF SURVEYS PER ZONE IS INDICATED BETWEEN BRACKETS.

The average number of birds per region per season is illustrated in figure 17. Low figures for zones 5 and 9, and for all zones during the summer period result at least partly from low counting effort. Higher values during autumn and spring are a consequence of migration from and to the wintering grounds. In zone 9, no differences between seasons can be observed. Near the coast and the Flemish Banks (zones 1-4) more species are found during the migration periods than elsewhere. When the summer data are not considered, the open sea areas (zones 7-9) have the smallest number of species. On average, the western Coastal Banks (zone 2) show a few more species than the eastern part (zone 1).

Highest N_1 -diversity is measured on the Coastal Banks and on/between the Flemish Banks (Fig. 18). The deepwater channel (zone 9) gives the lowest score, although this result is based on far less observations than elsewhere. Though no clear trend in diversity neither between different regions, nor between different seasons could be observed, values tend to be higher onshore compared to more offshore regions. Also, in offshore areas (zones 5-9) winter values are highest, summer diversity lowest and spring/autumn give intermediate situations, whereas regions 1-4 give a more mixed pattern. Finally, during the winter- and summer period when migration is minimal, the bank tops (zones 3,5 and 7) show lower diversity values than the gullies (zones 4,6 and 8) on all three bank systems.

We can conclude that on the BCS three main bird communities exist in terms of species diversity. The coastal stretch and the Flemish Banks are the richest, followed by the Zeeland Banks and the Hinder Banks with intermediate values, and finally the deep water zone with lowest figures (although a lower effort might have biased the results for zone 9). A lower diversity on the bank tops compared to the gullies can only be observed during winter and summer, when migration is minimal.

AVERAGE AVIFAUNA DIVERSITY PER ZONE

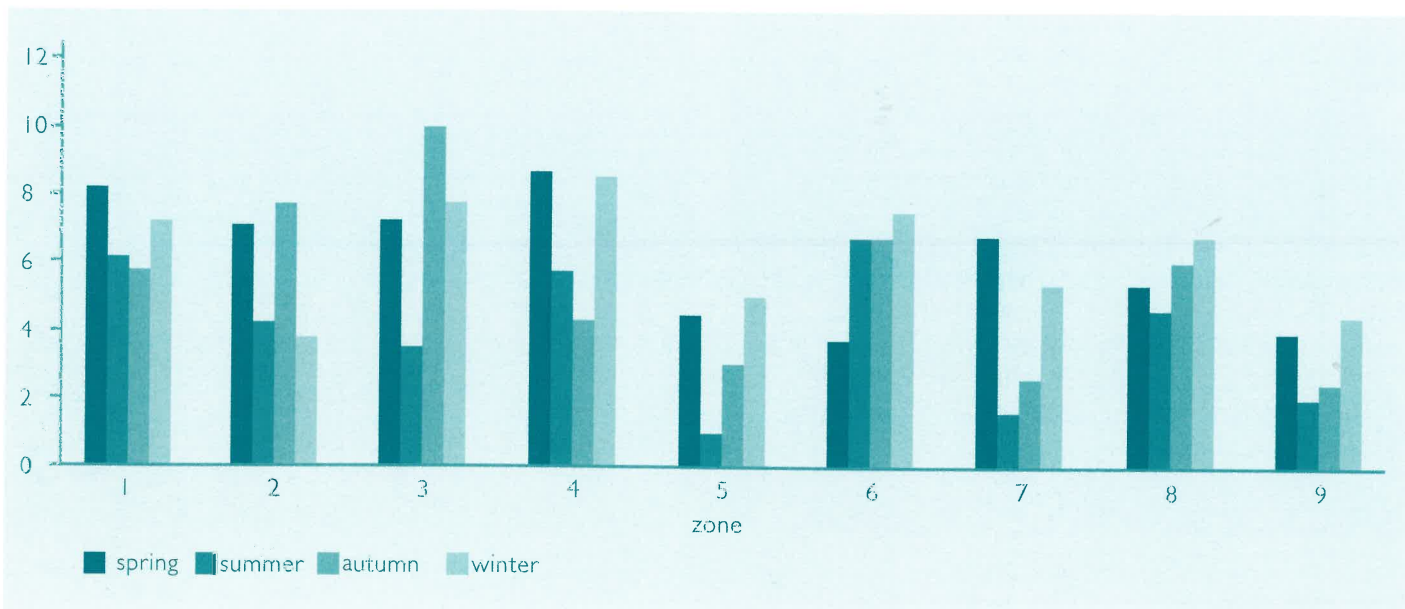


FIGURE 18. DIVERSITY (N_1) OF THE SEABIRD FAUNA PER REGION AND PER SEASON

8. GENE FLOW OF FISHES BETWEEN THE SOUTHERN BIGHT OF THE NORTH SEA AND THE ENGLISH CHANNEL

8.1. INTRODUCTION

The life history of many marine fishes is characterised by the presence of pelagic larvae whose potential for dispersal is strongly influenced by hydrodynamic forces such as diffusion, advection and mixing. Organism dispersal is the principal vector of genetic material (gene flow) and thus may be one of the major actors in shaping genetic structure. Non-random processes, which include an important behavioural component, such as larval retention and cohort fidelity (Sinclair 1988), selective migration, geographical structure (Ruzzante et al. 1998) and homing (Nielsen et al. 1999) limit diffusion. Consequently, the high potential for gene flow may not be fully realised. Marine fish maintain a subtle population structure in a seemingly homogenous but in fact structured ocean (Ward et al. 1994; Waples 1998). In addition, genetic structure is associated with contemporaneous and historic dispersal patterns. The latter refers to geological and palaeoclimatological processes during the Late Tertiary and Quaternary. Population expansion and reduction, sometimes in the very far past, has been embedded in the genome (Avice 1994). A second significant evolutionary force in marine organisms is selection on the numerous propagules, which are being released in the water column during each spawning population. Selective mortality exerts recurrent pressure on the genome of the fish larvae since survival rate is low. Each time only a fraction of the newly constituted larval genomes makes it to reproduction as adults. Nevertheless, most fish populations live in a dynamic genetic equilibrium. The life cycle of fish living either permanently or seasonally in the Southern Bight of the North Sea and the English Channel is modelled by the regional oceanography, geomorphology and palaeoecology. The region is structured most conspicuously by two physical gradients, one running on an onshore-offshore axis, the other one running parallel to the coast (MAFF 1981). The onshore-offshore axis shows a physical gradient from well-mixed turbid somewhat fresher coastal waters to clear oceanic higher salinity offshore water. The second gradient runs NE - SW with brackish water off the estuaries of the Great Rivers (Rhine, Schelde and Maas and to a lesser extent the Thames) and more saline water off the French and South English coast. The local, seasonal and interannual variability in temperature, salinity, density, turbidity, advection and vertical mixing influence the diversity of living organisms and the functioning of the food web. The question arises to what extent physical constraints imposed by the Dover Strait

model the local fauna. Indeed, it is generally accepted that Dover Strait separates the more northern temperate fauna from the southern temperate fauna (Ekman 1967; Longhurst 1998), which is well reflected in the distribution of sessile ascidian tunicates (Naranjo et al. 1998). In general, ichthyofauna diversity of the English Channel, which contains a great proportion of southern elements, is higher compared to the North Sea (Rogers et al. 1999). However, based on physical and faunistic arguments, this biogeographical separation is clinal without any indication of an abrupt discontinuity between both zones.

We test whether a dispersal barrier may be detected in the population genetic structure of demersal and pelagic bony fish spawning in the eastern English Channel and Southern Bight of the North Sea. If reduced or limited gene flow is detected, it may be indicative of limited contact between populations at both sides of Dover Strait, be it in the present or the past.

8.2. THE REGIONAL AND PALAEOCLIMATIC SETTING

The flow of the North Atlantic Current through the English Channel to the North Sea was reactivated after the last glaciation (12,000 y BP) when sea level rose and started to flood the area (Jones & Keen 1994). Until that time a low sea level and glaciers reduced the size of the North Sea to its deepest parts while the western English Channel represented an embayment of the Bay of Biscay. No glaciation of the Dover Strait has been reported although the climate was boreal such that a suitable ecological niche for the current fish fauna was not available. The intensity of the North Atlantic Current was not as strong during the last glacial period due to the presence of a fresh water layer in the North Atlantic (Mix et al. 1999). Today the flow of the North Atlantic Current varies interannually (Belgrano et al. 1998), which causes variable advection rates through Dover Strait, and hence variation in the chance of advection of southern faunas in the Southern Bight of the North Sea. The net residual current flows in a northerly direction, although it may reverse seasonally.

8.3. DEMERSAL SPECIES

In general, demersal fish species show more evidence of genetic structure than pelagic species (Grant & Bowen 1998). Although their planktonic larvae are prone to passive dispersal, (sub-adults live close to the bottom and eggs are often attached to the substrate. In general, the shallow depth of the North Sea and English Channel, strong tidal and wind driven mixing and high productivity favour the presence of demersal species. In order to test the validity of the hypothesis that Dover Strait limits gene flow, a list of those species whose genetic structure has been studied in either the eastern English Channel, the Southern Bight of the North Sea or in both regions was compiled by systematically screening for patterns in genetic differentiation and structure (Table 3). At least 70 species have been recorded in the area (Hayward & Ryland 1995) of which 14 species belonging to 10 families have been studied for their population genetic structure.

No study in the area has systematically targeted the genetic structure and most studies detail populations at a spatial scale of 1000 km or more. In addition, for each species, few samples were collected in the area and no attention was paid to temporal structure (with the exception of Child (1992)). The genetic structure of the flatfishes common sole (*Solea solea*) (Kotoulas et al. 1995; Exadactylos et al. 1998), turbot (*Scophthalmus maximus*) and brill (*S. rhombus*) (Blanquer et al. 1992), plaice (*Pleuronectes platessa*) (Galleguillos & Ward 1982) and flounder (*Pleuronectes flesus*) (Borsa et al. 1997) usually points to slight differences between adjacent populations, and increasingly larger genetic differences between populations located at some distance. Gradual variation is a common feature of many terrestrial and aquatic

organisms living in rather homogenous environments and has been called "isolation-by-distance" (Slatkin 1985). Alternatively, panmixis reflects the status when there is no evidence for genetic structure within the spawning population. In general, mature fish may move among neighbouring spawning grounds but are less likely to switch between widely separated spawning grounds despite their potential for large migrations. Plaice spawns in distinct populations in the English Channel and the North Sea (including the Hinder Banks). They may move hundreds of kilometres (Harden Jones 1968), and migrate seasonally through the Dover Strait (Arnold & Metcalfe 1995) but they tend to return faithfully to the same spawning area as documented with mark/recapture experiments (Metcalfe & Arnold 1997). Populations of plaice seem to be genetically discrete although this remains to be proven in the area (Galleguillos & Ward 1982). Since flounder shows limited genetic differentiation from the Baltic Sea to Portugal (including the North Sea), populations have reached equilibrium between gene flow and genetic drift (Borsa et al. 1997).

Spawning of the important species common sole is limited by the quality of the substrate, which seems reflected in the population nodes located about every 100 km (Kotoulas et al. 1995, Exadactylos et al. 1998). Exchange among stocks is limited as recorded from tagging experiments (Rijnsdorp et al. 1992). They spawn in the eastern English Channel and off the Belgian coast; larvae drift towards the coast in a north-eastern direction (Rijnsdorp et al. 1992).

Populations might have expanded recently and thus not have reached equilibrium. Genetic drift (which is the loss or tendency to fixation of alleles) might play a role especially in small-sized populations (Borsa et al. 1997).

Lack of genetic differentiation of the fish population does not always mean that there is a lack of genetic structure. Turbot for example shows a homogeneous genetic structure (which may point to panmixis), but its cestode parasite *Bothriocephalus gregarius* differentiates between the North Sea and the English Channel (Renaud et al. 1990). Thus, there is genetic isolation between these turbot populations. The closely related flatfish brill (*S. rhombus*) differentiates genetically between the English Channel and the North Sea (Blanquer et al. 1992).

Although gadoids are important and common members of the food web, especially in northern waters, only cod (*Gadus morhua*) (Arnason et al. 1992; Pogson et al. 1995) and to a lesser extent whiting (*Merlangius merlangus*) (Rico et al. 1997) have been studied. North-eastern Atlantic cod is abundant and sustains an important fishery. Populations genetically are weakly differentiated at the allozyme level while nuclear RFLP loci reveal an isolation-by-distance pattern (Pogson et al. 1995). The discrepancy between both markers is explained by a recent expansion in population size such that the population is not yet at equilibrium. Although no further details are provided by the authors, one of the possible scenarios is that cod recolonised the northern Atlantic Ocean at the end of the last glacial period. Whiting (*Merlangius merlangus*) is another important gadoid which shows limited genetic differentiation in the North Sea (Rico et al. 1997).

European eel (*Anguilla anguilla*) represents a peculiar case since its spawning grounds are located in the Sargasso Sea, while it matures in coastal and continental waters. The spawning aggregation represents a mixture of at least 3 spawning populations: an Icelandic population introgressed with American eel (*Anguilla rostrata*), a southern population and a central population (Daemen et al. submitted). There is a latitudinal cline along the European continental shelf as observed from allozyme markers, similarly to American and Japanese eel (Maes 1998). The reason remains unclear but it might be linked to selection, as allozyme markers may be evolutionary non-neutral. The Dover Strait does not seem to function as a barrier to this highly migratory species based on mitochondrial haplotypes of the eastern Atlantic population (Lintas et al. 1998; Daemen et al. submitted).

In the region, Atlantic salmon (*Salmo salar*) genetically belongs to the West-European clade that extends from northern Spain over the British Isles and Brittany to Denmark (e.g. Jordan et al. 1997). The species has suffered from the degradation of its freshwater habitat resulting in the loss of many populations. Adults migrate annually between feeding grounds in the North Sea and the English Channel to respectively more northern and southern breeding grounds. Elo (1993) established a genetic pattern of isolation by distance at a scale of several thousand kilometres reflecting a poor genetic differentiation. River populations are phenotypically highly distinct and well adapted to local conditions (Nielsen et al. 1999). Another anadromous salmonid, the brown trout (*Salmo trutta trutta*), has similarly suffered from habitat loss. West-European spawning populations are typically fragmented by river basin (Krieg & Guyomard 1985, Bernatchez et al. 1992).

Few non-commercial (read small sized) fishes of the area have been studied. Goby (*Pomatoschistus* sp.), dragonet (*Callionymus* sp.), bib (*Trisopterus luscus*), pipefish (Syngnathidae), sandeel (*Ammodytes tobianus*) and lesser weever (*Echiichtys vipera*) play a key role in coastal and offshore food webs. They may reach high densities and represent important links between benthos production and the larger commercial species. In general, their small size suggests dispersal on small scales, while demersal behaviour limits them to specific habitats. Some differences have been observed between populations of the common goby, *Pomatoschistus microps*, at one side those residing in the Southern Bight and the English Channel, and at the other side those residing along the eastern Atlantic Ocean (Al-Hassan et al. 1987). Common gobies of the Teign estuary (Devon, English Channel) had a change at PGI-A allele frequencies with increasing modal age which might be attributed to genetic selection with selected alleles being favoured under specific conditions. Year after year, the newly recruited goby larvae are subjected to non-random high mortality. It remains to be shown what the relative contribution is of such recent and more historic processes. Our preliminary findings point to the rather homogenous phylogeography of the sand goby (*Pomatoschistus minutus*) living in the Southern Bight of the North Sea. Wallis & Beardmore (1984) observed a link between goby genetic heterozygosity and environmental heterogeneity. Coastal

species (such as the common goby), living in a more variable environment, have higher levels of genetic variation, while offshore species (such as the painted goby *P. pictus*), living in a more stable marine environment, have lower genetic variability.

The genetic differentiation of the anadromous threespined stickleback (*Gasterosteus aculeatus*) is polarised in an offshore – inshore direction with inland populations progressively differentiating from coastal populations (isolation-by-distance). Across the Holarctic, marine and anadromous threespined sticklebacks have colonised inland waters several times independently. This unique pattern has been called a raceme structure (Bell & Andrews 1997). Within the North Sea, coastal populations seem to differentiate to a certain degree but the lack of sufficient sample coverage complicates the interpretation (Buth & Haglund 1994, Orti et al. 1994). An important issue is the genetic impact of the intensive trawling fishery (Rogers et al. 1999). Heavily fished species (such as common sole, plaice and cod) might suffer from the loss of fast growing population members since they are likely to be caught first. Rijnsdorp (1993) analysed somatic growth, sexual maturity and fecundity of plaice (*Pleuronectes platessa*) from historic fisheries data. Despite the fishing pressure the reproductive strategy changed only marginally since 1900. Rijnsdorp (1993) suspects that the observed reduction in length-at-first-maturity includes a genetic component. Otherwise said, plaice has today a tendency to spawn at younger age. Cod stocks are thought to be imploding (Cook et al. 1997), but the genetic consequences have been incompletely documented since the complexity of phenotypic selection hampers analysis. In an extensive study of the North Atlantic cod stocks, including the Southern Bight of the North Sea on the basis of the locus haemoglobin, a deficit in heterozygotes was observed which could point to selection pressure (Jamieson & Birley 1989).

8.4. PELAGIC SPECIES

The pelagic fishery represents a fraction of the total Belgian fish landings. The poor economic significance is reflected in the few genetic studies of pelagic species in the region. Grant (1984) and Joerstad et al. (1991) concluded from allozymes and Dahle & Eriksen (1990) from mtDNA RFLP that North Sea herring populations hardly differentiate genetically, although considerable phenotypic differences may be observed (including morphological and spawning traits). Herring aggregate at specific spawning locations, which are directly related to the local hydrodynamics while larvae drift in response to wind advection (Bartsch et al. 1989). The dynamic gene flow among spawning populations counters genetic differentiation, but conserves some phenotypically adaptive traits (Turan et al. 1998).

The Atlantic population of sea bass (*Dicentrarchus labrax*) spawns along the Atlantic coast at specific sites. The source of the Belgian population (largely consisting of juvenile and subadult fish) has not been established; they spawn either in the central English Channel or in the Thames Estuary. Child (1992) observed differences between populations from the Irish Sea and the Channel/North Sea at the allozyme PGM locus but Naciri et al. (1999) could not find distinct microsatellite DNA differences all along from the Strait of Gibraltar to the North Sea. More interestingly, lagoonal/estuarine and coastal populations of sea bass are under different selection pressure with lagoonal juvenile fish showing different allozyme frequencies at selected loci (Lemaire et al. submitted).

8.5. CONCLUSIONS

Ward et al. (1994) observed that marine fishes had a lower level of genetic differentiation in comparison to fresh water species; anadromous species (such as salmon and shad) take an intermediate position. The lack of absolute barriers at sea and the contribution of stratification, upwelling, fronts and eddies reduce the chances of genetic isolation although species with discrete spawning stocks have higher chances of differentiating genetically. Moreover, life-history traits (related to spawning, behaviour, survival and selective mortality) model the genetic structure. In case of the Belgian Continental Shelf, the limited information available points to continuity between fish populations of the English Channel, the Southern Bight of the North Sea and the Central North Sea. Dispersal by local hydrodynamics seems to dominate over biological traits in the area. Directed sampling, which takes in account the species-specific population dynamics and ecology, as well as the use of high-resolution markers (such as microsatellites), should clarify this conclusion. It remains unclear what the impact is of the last glaciation, but it may be that many species have reinvaded the area from a refuge located in the South-eastern Atlantic Ocean (Gulf of Biscay). Given the relatively short time since colonisation, this has been insufficient to develop strong differences at both sides of the Dover Strait. Finally, the influence of the intensive fishery on the genetic potential shouldn't be underestimated, since the fishing mortality of for example sole may reach 50% on the Belgian Continental Shelf.

9. A PRELIMINARY CHECK LIST OF INFECTIOUS EUKARYOTES (PARASITES) OF FISHES FROM THE BELGIAN CONTINENTAL SHELF

9.1. INTRODUCTION

Infectious diseases and more specifically parasites play a crucial role in the population dynamics of invertebrates and vertebrates (May & Anderson 1983). The regulation and genetic selection of natural host populations is influenced by the dynamics and heterogeneity of the environment, inter-specific interactions (predation, competition, infections by viruses, bacteria and parasites) and intraspecific interactions (cannibalism and competition). Interesting is that the biology of the parasite is tightly linked to life history traits of the intermediate and final host. Co-evolution, which has been described as a continuous biological arms race, and co-speciation occur commonly.

Marine fish parasites principally belong to five taxa (Fungi, Protozoa, Platyhelminthes, Nematoda and Crustacea). Viruses and infectious Bacteria, which may be considered as parasites and play crucial roles in the marine food web, are for practical reasons excluded from this review. Since a systematic inventory of the fish parasites and their hosts of the Belgian Continental Shelf doesn't exist, we attempted to compile records scattered throughout the refereed and non-refereed (grey) international literature, including some records from last century. The checklist is complicated by the ambiguous status of many taxa.

9.2. PRELIMINARY CHECKLIST

FUNGI: There is only one species record, *Ichthyophus haferi*, which has been observed on whiting (Declerck, pers comm.)

PROTOZOA: The first records have been documented by Van Beneden (1871). His data have not been included in this review because of their historic value and taxonomic uncertainty. Many species are infected by *Glugea stephani* (Microsporidia) (Declerck 1993; 1998; Geets 1986; Van Damme 1985). *Haemogregarina simondi* (Sporozoa) infects the erythrocytes of common sole (*Solea solea*) and Atlantic cod (*Gadus morhua*) (Declerck, pers comm.). Van Damme (1985) found *Trichodina* sp. on the gills of plaice.

MONOGENEA: infect a single host. The first records have been documented by Van Beneden (1871) but his data have not been included because of their historic value and uncertainty on the taxonomy. Several genera

have been observed of which the genus *Gyrodactylus* includes more than 400 species (Malmberg 1998). The local inventory mentions *G. arcuatus* which parasitizes threespined stickleback (*Gasterosteus aculeatus*), *G. micropsi*, *G. forma minutus*, *G. forma pictus* and *G. longidactylus* which parasitize amongst others gobies of the genus *Pomatoschistus* (Geets et al. in prep.). Important spatio-temporal differences in population dynamics and host specificity have been observed. *Diclidophora* infects the gills of bib *Trisopterus. minutus* (*D. minuti*) and *T. luscus* (*D. luscae*) (Tirard et al. 1992).

TREMATODA / DIGENEA: infect an intermediate and a final host. *Cryptocotyle lingua* is a general parasite with sprat (*Sprattus sprattus*) and greater sand eel (*Hyperoplus lanceolatus*) as intermediate host and carnivorous fish and birds as final host (Declerck 1992a; 1998; Groenewold et al. 1996). *Asymphylodora demeli* is a final host of gobies of the genus *Pomatoschistus* (Hamerlynck et al. 1989). *Derogenes varicus* has been found in gobies of the genus *Pomatoschistus* (Geets, pers. comm.). *Zoogonoides viviparus* is a common parasite of plaice in the Southern Bight of the North Sea (Wickins & Macfarlane 1973). *Aphalloides coelomicola* infects the common goby (Vaes 1978).

CESTODA: are also characterised by an intermediate and final host. Pierre-Joseph Van Beneden compiled his observations along the Belgian coast in two studies (1850, 1864). The tapeworm *Bothriocephalus scorpii* infects *Pomatoschistus* as intermediate host (Hamerlynck et al. 1989) and turbot (*Scophthalmus maximus*) as final host (de Groot 1971). *B. gregarius*, which also infects turbot, shows genetic differences between the North Sea and the English Channel (Renaud et al. 1990).

NEMATODA: : *Anisakis simplex* infects Atlantic herring as intermediate host and *A. pseudoterranova* (cod worm) whiting and cod on the Belgian Continental Shelf (Davey 1972; Rae 1972; Declerck, pers. comm.); whales are each time the final host. The intensity of the infection coincides with the occurrence of the host (Van Banning & Becker 1978). *Hysterothylacium aduncum* occurs in the abdominal cavity of *Pomatoschistus* gobies (Hamerlynck et al. 1989). *Cuculanus heterochrous* occurs in plaice and dab (*Limanda limanda*) collected in the Southern Bight of the North Sea (Geets 1986; Van Damme 1985; Wickins & Macfarlane 1973). *Contracaecum aduncum* infects the body cavity of plaice and dab (Geets 1986; Van Damme 1985) and the stomach of *Pomatoschistus* gobies (Fonds, pers. comm.). *Capillaria wickinsi* generally infects plaice (Van Damme 1985; Wickins & Macfarlane 1973).

CRUSTACEA: The first detailed observations on the crustacean parasites of the Belgian Continental Shelf have been made by Pierre-Joseph Van Beneden (1861). *Tripaphilus* (*Lerneonema*) *musteli* (Van Beneden, 1851) was observed on smooth hound (*Mustelus mustelus*) and the new copepod genus *Kroyeria lineata* on unspecified fishes (Van Beneden, 1853a). The genus *Eudactylina acuta* was observed on the shark *Squalus acanthias* for the first time (Van Beneden, 1853b). The distribution, morphometry, cycle and host specificity of *Lernaeocera branchialis* and *L. lusci* (junior synonym of *L. minuta*) has been described by Declerck (1992a,b, 1993 and 1998), Van Damme & Hamerlynck (1992), Van Damme et al. (1992, 1994, 1996 and 1997) and Van Damme & Ollevier (1994, 1995 and 1996). The infection dynamics of *L. branchialis* on O+ whiting are characterised by an infection peak in late spring and in fall. Infection of the adult sand goby *Pomatoschistus minutus* by *L. lusci* occurs in spring; in early summer the parasites become adult while most hosts die in July after spawning. There are possibly three forms of *L. lusci* (*f. lusci* on whiting, *f. minuta* on *Pomatoschistus* and *f. lyra* on dragonet) which affect the metabolism (hematocrit titre) of the final host. *Lepeophtheirus pectoralis* occurs commonly on plaice of the Southern Bight of the North Sea (Wickins & Macfarlane 1973). *Acanthochondria cornuta* is found in the gill cavity of plaice (Van Damme 1985). The isopod *Rocinela danmoniensis* occurs rarely on whiting (Declerck, pers. med.).

In total, we report 32 parasite taxa, which by no means represent the complete inventory. For comparison, Boxshall (1974) observed 39 parasitic copepods on 41 fish species in the western North Sea. Groenewold et al. (1996) observed a narrow link between parasite (22 species) and host (4 small and middle-sized fish species) from the diet of the host in the Wadden Sea.

9.3. CONCLUSION

Eukaryotic parasites may be studied from two perspectives. They regulate populations by affecting fitness and in selected cases survival, and they are markers of the host by providing insight in his historic and current movements. The latter is useful to study phylogeny, population dynamics and genetic structure (phylogeography) since knowledge of the genotypes of host and parasite provides a double marker system. Genetic research on marine parasites in the English Channel and the Southern Bight of the North Sea is limited to the Monogenea *Gyrodactylus* (Cunningham 1997; Zietara et al. submitted), the Cestoda *Diclidophora* (Tirard et al. 1992) and *Bothriocephalus* (Renaud et al. 1986, 1990). Tirard (1991) and Van Damme (pers. comm.) observed genetic differences in the copepod *Lernaeocera* without providing further details. Nevertheless, issues such as the evolution of the local fish fauna as well as genetic selection on the heavily fished fish populations could be addressed in this manner. Fluctuations in the quality and quantity of the fish fauna of the North Sea have been attributed to climate variations and overfishing. The contribution of each remains unclear, but an important structuring force of the fish populations might be apart from food, the impact of infections by viruses, bacteria and parasites. The general lack of knowledge in these fields hampers a conclusion in regards to spatio-temporal occurrence, population dynamics, ecology and population genetics.

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PRELIMINARY SPECIES LIST OF THE BELGIAN CONTINENTAL SHELF

All species lists of the referred publications have been compiled to produce this preliminar list of benthos, bird and fish parasite species that have been recorded over the past thirty years. Since the bird counting also resulted in censuses of marine mammals, those observations have been included here as well.

This list can only serve as starting point to complete the full species list for the BCS. Observation made before 1970 have not been included. Data collected in the intertidal zone of our coast have also not been included. The list needs further updating with unpublished observations of other research groups and of those of amateur biologists.

Dutch names have been supplied where possible.

The species list of the fish parasites has been given in the text.

NEMATODA

(spoelwormen)

Actinonema celtica
Euchromadora sp. 1
Chromadorita n. sp. 1
Chromadorita n. sp. 2
Chromadorita sp. 3
Chromadorita sp. 4
Dichromadora cucullata
Dichromadora hyalocheile
Dichromadora sp. 1
Graphonema sp. 1
Hypodontolaimus trichophora
Hypodontolaimus n. sp. 1
Innocuema tentabunda
Chromadorella salicaniensis
Chromadorella problematica
Karkinochromadora lorenzi
Neochromadora angelica
Neochromadora munita
Neochromadora paratecta
Neochromadora poecilosoma
Neochromadora n. sp. 1
Prochromadorella attenuata
Prochromadorella ditlevseni
Prochromadorella longicaudata
Prochromadorella sp. 1
Prochromadorella sp. 2
Ptycholaimellus sp. 1
Rhips ornata
Spiliphora aff. *dolichura*
Spilophorella paradoxa
Gomphonema sp. 1
Nannolaimoides sp. 1
Nannolaimus *fusus*
Nannolaimus aff. *gutatus*
Nannolaimus sp. 1
Nannolaimus sp. 2
Paracanthonchus longus
Paracanthonchus thauasius
Paracanthonchus sp. 2
Paracyatholaimus occultus
Paracyatholaimus pentodon
Paracyatholaimus sp. 1
Paracyatholaimus sp. 2
Paracyatholaimoides assymetricus
Paracyatholaimoides labiozetosus
Paralongicyatholaimoides macramphus
Paralongicyatholaimoides sp. 1
Phyllolaimus tridentatus
Pomponema ammophilum
Pomponema carinatum
Pomponema coomansi
Pomponema elegans
Pomponema loticum
Pomponema multipapillatum
Pomponema sedicima
Pomponema tautrense
Pomponema sp. 1
Pomponema sp. 2
Pomponema sp. 3
Choniolaimus papillatus
Choniolaimus sp. 1
Gammanema conicauda
Gammanema rapax
Gammanema n. sp. 1

Gammanema sp. 1
Halichoanolaimus sp. 1
Latronema aberrans
Latronema orcinuma
Latronema sp. 1
Richtersia deconincki
Richtersia inaequalis
Synonchiella riemanni
Synonchiella n. sp. 1
Chromaspirina chabaudi
Chromaspirina inglisi
Chromaspirina parapontica
Chromaspirina pellita
Chromaspirina n. sp. 1
Chromaspirina n. sp. 2
Desmodora pontica
Desmodora sanguinea
Desmodora schulzei
Desmodora tenuispiculum
Desmodora n. sp. 1
Stygodesmodora epixantha
Eubostrichus n. sp. 1
Molgolaimus cuanensis
Molgolaimus turgofrons
Molgolaimus n. sp. 1
Leptonemella aphanothecae
Metachromadora quadribulba
Onyx perfectus
Pseudonchus decempapillatus
Pseudonchus sp. 1
Pseudodesmodora n. sp. 1
Sigmophoranema rufum
Spirinia laevis
Spirinia parasitifera
Spirinia sp. 1
Epsilonema pustulatum
Epsilonema serrulatum
Metepsilonema calaisi
Metepsilonema emersum
Metepsilonema hagmeieri
Perepsiloma crassum
Dracognomus tinae
Prochaetosoma mediterranicum
Pareudraconema sp. 1
Bolbolaimus dentatus
Bolbolaimus riemanni
Bolbolaimus teutonicus
Bolbolaimus sp. 1
Calomicrolaimus acanthus
Calomicrolaimus honestus
Calomicrolaimus monstrosus
Calomicrolaimus parahonestus
Calomicrolaimus n. sp. 1
Calomicrolaimus sp. 2
Cinctonema sp. 1
Ixonema sordidum
Microlaimus acinaces
Microlaimus annelisiae
Microlaimus conothelis
Microlaimus cyatholaimoides
Microlaimus marinus
Microlaimus ostracion
Microlaimus sp. 1
Monoposthia mirabilis
Nudora n. sp. 1
Rhinema sp. 1
Alaimella cincta

Anomonema deconincki
Camacolaimus longicaudata
Camacolaimus tardus
Camacolaimus sp. 1
Dagda bipapillata
Aphanolaimus sp. 1
Halaphanolaimus harpaga
Halaphanolaimus longisetosus
Halaphanolaimus sp. 1
Leptolaimoides sp. 1
Leptolaimus sp. 1
Stephanolaimus bicoronatus
Stephanolaimus elegans
Stephanolaimus gandavensis
Rhadinema flexile
Tarvaia sp. 1
Aegialolaimus tenuicaudatus
Cyarttonema elegans
Cyarttonema zostera
Ceramonema yunfengi
Ceramonema sp. 1
Ceramonema sp. 4
Dasyrella sp. 1
Dasyneimoides albaensis
Dasyneimoides sp. 1
Metadasyneimoides latus
Metadasyneimoides aff. *longicollis*
Metadasyneimoides n. sp. 1
Metadasyneimoides sp. 2
Pselionema longissimum
Pselionema sp. 1
Tubolaimoides aff. *tenuicaudatus*
Diplolaimella sp. 1
Monhystera aff. *macrura*
Monhystera disjuncta
Monhystera sp. 1
Monhystrella parelegantula
Amphimonhystera anechma
Amphimonhystrella sp. 1
Cobbia trefusiaformis
Daptonema fistulatum
Daptonema flagellicaudata
Daptonema hirsutum
Daptonema kornoeense
Daptonema nanum
Daptonema normandicum
Daptonema proprium
Daptonema riemanni
Daptonema stylosum
Daptonema svalbardense
Daptonema tenuispiculum
Daptonema trichinus
Daptonema xyaliforme
Daptonema sp. 1
Daptonema sp. 3
Daptonema sp. 4
Daptonema sp. 5
Echinotheristus teutonicus
Gonionchus cumbraensis
Gonionchus longicaudatus
Gonionchus heipi
Metadesmolaimus aduncus
Metadesmolaimus pandus
Linhystera
Paramonhystera pellucida
Rhynchonema ceramatos
Rhynchonema falciferum

Rhynchonema lyngei
Rhynchonema megamhida
Rhynchonema moorea
Rhynchonema quemer
Rhynchonema scutatum
Rhynchonema n. sp. 1
Rhynchonema sp. 1
Stylotheristus mutilis
Theristus denticulatus
Theristus flevensis
Theristus heterospiculoides
Theristus pertenuis
Theristus roscoffiensis
Theristus scanicus
Theristus sp. 1
Theristus sp. 2
Theristus sp. 4
Trichotheristus mirabilis
Valvaelaimus major
Xyala imparis
Xyala striata
Sphaerolaimus balticus
Sphaerolaimus gracilis
Desmoscolex frontalis
Desmoscolex longisetosus
Desmoscolex n. sp. 1
Desmoscolex sp. 2
Paratricoma sp. 1
Tricoma brevisstris
Tricoma polydesma
Tricoma steineri
Tricoma n. sp. 1
Tricoma n. sp. 2
Tricoma n. sp. 3
Tricoma n. sp. 4
Tricoma sp. 6
Tricoma sp. 7
Tricoma sp. 9
Tricoma sp. 10
Tricoma sp. 11
Tricoma sp. 12
Tricoma sp. 14
Tricoma sp. 15
Tricoma sp. 17
Siphonolaimus ewensis
Linhomoeidae sp. 1
Linhomoeidae sp. 2
Desmolaimus zeelandicus
Desmolaimus sp. 1
Megadesmolaimus sp. 1
Eleutherolaimus amasi
Eleutherolaimus iniquisetosus
Eleutherolaimus sp. 1
Eleutherolaimus stenosoma
Metalinhomoeus n. sp. 1
Metalinhomoeus sp. 2
Metalinhomoeus sp. 3
Terschellingia longicaudata
Linhomoeus elongatus
Linhomoeus filaris
Paralinhomoeus filiformis
Paralinhomoeus lepturus
Paralinhomoeus sp. 1
Ascolaimus sp. 1
Axonolaimus helgolandicus
Axonolaimus orcombensis
Odontophora paravilloti

Odontophora phalarata
Odontophora exharena
Odontophora sp. 1
Odontophora sp. 2
Odontophora sp. 3
Odontophoroides paramonhystera
Synodontium sp. 1
Sabatieria armata
Sabatieria celtica
Sabatieria longispinosa
Sabatieria rota
Sabatieria punctata
Sabatieria sp. 1
Setosabatieria hilarula
Paramesonchium belgium
Araeolaimoides sp. 1
Campylaimus sp. 1
Diplopeltula botula
Diplopeltula n. sp. 1
Diplopeltula n. sp. 2
Diplopeltula sp. 3
Diplopeltula sp. 5
Pararaeolaimus nudus
Southerniella zosteræ
Southerniella sp. 1
Trileptium parisetum
Enoploides spiculohamatus
Enoploilaimus conicollis
Enoploilaimus longicaudatus
Enoploilaimus propinquus
Enoploilaimus zosteræ
Enoploilaimus sp. 1
Mesacanthion africanthiforme
Mesacanthion diplechma
Mesacanthion hirsutum
Mesacanthion sp. 1
Oxyonchus dentatus
Oxyonchus sp. 1
Paramesacanthion sp. 1
Anoplostoma sp. 1
Chaetonema sp. 1
Chaetonema sp. 2
Anticoma acuminata
Thalassironus sp. 1
Synonchus brevisetosus
Oxystomina sp. 1
Thalassoalaimus tardus
Thalassoalaimus sp. 1
Wieseria pica
Wieseria sp. 1
Halalaimus aff. florescens
Halalaimus sp. 1
Halalaimus sp. 2
Halalaimus sp. 3
Halalaimus sp. 4
Halalaimus sp. 5
Pelagonema sp. 1
Oncholaimellus sp. 1
Viscosia coomansi
Viscosia franzzii
Viscosia glabra
Viscosia langrunensis
Viscosia separabilis
Viscosia viscosa
Viscosia n. sp. 1
Viscosia n. sp. 2
Viscosia sp. 1
Viscosia sp. 2
Viscosia sp. 3
Metoncholaimus scanicus
Metoncholaimus sp. 1
Oncholaimus campyloceroides
Oncholaimus aff. attenuatus
Calyptronema maxweberi
Eurystomina ornata
Eurystomina sp. 3

Pareurystomina sp. 1
Polygastrophora sp. 1
Bathylaimus capacosus
Bathylaimus parafllicaudatus
Bathylaimus paralongisetosus
Rhabdodemanian birgittæ
Rhabdodemanian minor
Rhabdodemanian sp. 1
Pandolaimus sp. 1
Rhabdocoma americana
Rhabdocoma minor
Trefusia n. sp. 1
Lauratonemoides sp. 1

PHORONIDA

Phoronida spec

CNIDARIA

Bougainvillea brittanica
Mitrocornella polydiademata

CTENOPHORA

(kamkwallen)
Pleurobachia pileus
Beroe cucumis
Beroe gracilis
Beroe sp.

CHAETOGNATHA

(pijlwormen)
Sagitta elegans

POLYCHAETA

(borstelwormen)
Harmathoe lunulata
Harmathoe ljunmani
Harmathoe nodosa
Harmathoe speceis
Eunoe nodosa
Sigalion mathildæ
Pholoe minuta
Pholoe inorata
Sthenelais boa
Pisione remota
Eteone longa
Eteone flava
Eteone lactea
Mystides limbata
Protomystides sp.
Hesionura augeneri
Phyllodoce laminosa
Phyllodoce sp.
Anaitides groenlandica
Anaitides mucosa
Anaitides maculata
Anaitides lineata
Anaitides subulifera
Eumida sanguinea
Eumida bahusiensis
Microphthalmus similis
Microphthalmus listensis
Syllis gracilis
Typosyllis variegata
Typosyllis armillaris
Eusyllis blomstrandii
Streptosyllis websteri
Streptosyllis arenæ
Opisthodontia pterochaeta
Sphaerosyllis hystrix
Syllidae sp.
Exogone verugera
Exogone naidina
Exogone hebes
Autolytus prolifer
Autolytus edwardsi
Autolytus sp.
Nereis succinea

Nereis longissima
Nephtys cirrosa (zager)
Nephtys hombergii (zager)
Nephtys longosetosa (zager)
Nephtys caeca (zager)
Nephtys incisa (zager)
Nephtys sp. (zager)
Glycera capitata
Glycera alba
Glycera convoluta
Glycinde nordmanni
Goniadella bobretzkii
Lumbrineris gracilis
Lumbrineris latreilli
Dorvillea caeca
Dorvillea neglecta
Protodorrvillea kefersteini
Scoloplos armiger
Aricidea minuta
Paraonis fulgens
Poecilochaetus serpens
Spio filicornis
Spio sp.
Polydora ciliata
Polydora pulchra
Polydora ligni
Polydora sp.
Pygospio elegans
Spiophanes bombyx
Spiophanes kroyeri
Aonides oxycephala
Aonides paucibranchiata
Scolecopsis bonnierii
Scolecopsis squamata
Malacoceros vulgaris
Magelona papillicornis
Caulierella alata
Tharyx marioni
Cirratulus filiformis
Chaetozone setosa
Macrochaeta helgolandica
Cirratulidae sp.
Ophelia limacina
Euzonus flabelligerus
Travisia forbesii
Capitella capitata
Capitomastus minimus
Capitellidae sp.
Notomastus latericeus
Heteromastus filiformis
Praxillura longissima
Owenia fusiformis
Pectinaria koreni
Lanice conchilega (zandkokerworm)
Polycirrus medusa
Polycirrus sp.
Pomatoceros triquetus
Oriopsis armandi

ARCHIANELLIDA

Protodrillus chaetifer
Protodrillus sp.
Polygordius appendiculata
Saccocirrus papillocercus
Saccocirrus sp.

OLIGOCHAETA

Grania postclitellochaeta
Oligochaeta sp.

NEMERTINA

Nemertini sp.

SIPUNCULIDA

Sipunculid sp.

CEPHALOPODA

Sepioida atlantica (kleine zeekat)
Sepia officinalis (zeekat)
Loligo vulgaris (pijlinktvis)
Allotheutis subulata (kleinepijlinktvis)

GASTROPODA

(slakken)
Leptochiton asellus (keverslak)
Crepidula formicata (muiltje)
Nassarius reticulatus (fuikhoorn)
Lunatia alderi (glanzende tepelhoorn)
Caecum glabrum

BIVALVIA

(schelpen)
Striarca lactea (melkwitte arkschelp)
Modiolus modiolus (paardemossel)
Mytilus edulis (blauwe mossel)
Goodallia triangularis (kleine astarte)
Barnea candida (witte boormossel)
Tellimya feruginosa (ovale zee-klitschelpje)
Mysella bidentata (tweetand-schelpje)
Cerastoderma edule (kokkel)
Chamelea striatula (venusschelp)
Venerupis pullastra (tapijtschelp)
Petricola pholadiformis (amerikaanse boormossel)
Macra corralina (grote strand-schelp)
Spisula solida (stevige strand-schelp)
Spisula elliptica (ovale strand-schelp)
Spisula subtruncata (halfgeknotte strandschelp)
Spisula sp.
Donax vitatus (zaagje)
Angulus pygmaeus (kleine platschelp)
Angulus fabula (rechtsgetreepte platschelp)
Angulus tenuis (tere platschelp)
Macoma baltica (nonnetje)
Abra nitida
Abra prismatica (prismatische dunschaal)
Abra alba (witte dunschaal)
Ensis arcuatus (grote zwaard-schede)
Ensis ensis (slanke kleine zwaard-schede)
Ensis sp.
Phaxas pellucidus (sabelschede)
Sphenia binghami
Thracia papyracea
Aequipecten opercularis (wijde mantel)

PYCNOGONIDA

(zeespinnen)
Nymphæa rubrum
Achelina longipes
Phoxichilidium femoratum
Endeis laevis
Pycnogonum littorale

HARPACTICOIDEA

Longipedia minor
Canuella perplexa
Arenosetella germanica
Ectinosoma melaniceps
Ectinosoma sp. 1
Halectinosoma gothiceps

Halectinosa hermani
Halectinosa propinquum
Halectinosa sarsi
Halectinosa sp. 1
Hastigerella leptoderma
Pseudobradia beduina
Pseudobradia minor
Pseudobradia similis
Pseudobradia sp. 1
Ectinosomatidae sp. indet.
Euterpina acutifrons
Microarthridion littorale
Thompsonula hyaenae
Scutellidium australe
Tisbe furcata
Alteutha depressa
Dactylopedella flava
Dactylopedella tisboides
Dactylopedella vulgaris
Amphiascoides debilis
Amphiascus parvus
Apmiascus varians
Bulbamphiaseus imus
Bulbamphiaseus inermis
Paramphiascella vararensis
Paramphiascopsis longirostris
Psammotopa phyllosetosa
Ameira brevipes
Ameira hyalina
Ameira parvula
Interleptomesochra eulitoral
Proameira psammophyla
Proameira sp. 1
Psyllocamptus minutus gelatinosus
Sarsameira peresi
Sicameira leptoderma
Ameiridae spp.
Apodopsyllus littoralis
Apodopsyllus sp. 1
Diarthrodella secunda
Kliopsyllus constrictus
Kliopsyllus holsaticus
Kliopsyllus paraholsaticus
Paramesochra helgolandica
Paramesochra mielkei
Scotopsyllus minor
Scotopsyllus aff. minor
Scotopsyllus sp. 1
Scotopsyllus sp. 2
Scotopsyllus sp. 3
Scotopsyllus intermedius
Paramesochridae gen. 1 sp. 1
Mesochra pygmaea
Arenocaris bifida
Arenopontia sp. 1
Cylindropsyllus remanei
Evansula pygmaea
Leptastacus laticaudatus
Leptopontia curvicauda
Paraleptastacus espinulatus
Paraleptastacus holsaticus
Paraleptastacus spinicauda
Psammastacus remanei
Enhydrosoma propinquum
Cletodidae sp.
Esola bulligera
Laophonte pygmaea
Laophonte danversae
Laophontopsis lamellifera
Metacyclopsina brevisetosa

CALANOIDEA

Centropages typicus
Temora longicornis
Calanus helgolandicus
Caligidae sp.

EUPHAUSIACEA (krill)

Nyctiphanes couchi

MYSIDACEA (aasgarnalen)

Siriella armata
Gastrosaccus spinifer
Mysidopsis gibbosa
Paramysis arenosa
Schistomysis kervillei
Schistomysis spiritus
Praunus flexuosus
Mesopodopsis slabberi
Neomysis integer (brakwateraasgarnaal)
Acanthomysis longicornis

CUMACEA (zeekomma's)

Cumopsis goodsiri
Cumopsis sp.
Iphinoe trispinosa
Pseudocuma longicornis
Pseudocuma similis
Pseudocuma gilsoni
Pseudocuma sp.
Bodotria arenosa
Bodotria scorpioides
Bodotria pulchella
Diastylis rugosa
Diastylis laevis
Diastylis bradyi
Diastylis rathkei

TANAIDACEA

Tanaissus lilljeborgi
Pseudoparatanais batei

ISOPODA (pissebedden)

Prodajus ostendensis
Eurydice spinigera
Eurydice affinis
Eurydice pulchra (strandpissbed)
Idotea linearis
Idotea pelagica

AMPHIPODA (vlokkreeften)

Hippomedon denticulatus
Orchomene nana
Orchomene sp.
Tmetonyx similis
Scopelocheirus hopei
Ampelisca brevicornis
Panoploea minuta
Amphilocheus manudens
Amphilocheus neapolitanus
Leucothoe lilljeborgi
Leucothoe incisa
Stenothoe marina
Talorchestia brito (strandvlo)
Gammarus crinicornis
Gammarus sp.
Cheirocratus sundevalli
Cheirocratus intermedius
Cheirocratus sp.
Melita palmata
Melita obtusata
Bathyporeia guilliamsoniana
Bathyporeia pelagica
Bathyporeia elegans
Bathyporeia sp.
Haustorius arenarius
Urothoe poseidonis
Urothoe brevicornis
Urothoe marina
Urothoe elegans
Urothoe sp.
Perioculodes longimanus
Pontocrates altamarinus
Pontocrates arenarius

Synchelidium haplocheles
Megaluropus agilis
Melphidippa macra
Apherusa ovalipes
Apherusa bispinosa
Apherusa sp.
Pleusymtes glaber
Atylus falcatus
Atylus swammerdami
Aora typica
Microprotopus maculatus
Corophium volutator (slijkgarnaal)
Corophium arenarium
Corophium sextonae
Corophium ascherusicum
Corophium bonelli
Unciola planipes
Jassa falcata
Hhyperia galba
Pariambus typicus (hongerlijder)
Phthisica marina (spookkreeftje)

DECAPODA

Palaemon elegans (gewone steurkrab)
Palaemon serratus
Alpheus glaber
Hippolyte varians
Thorulus cranchii
Processa canaliculata
Processa modica (parva)
Pandalina brevirostris
Pandalus montagui (ringsprietgarnaal)
Crangon crangon (gewone garnaal)
Crangon allmani
Philocheras trispinosus
Callinassa subterranea
Callinassa tyrrhena
Callinassa sp.
Upogebia deltaura
Galathea intermedia
Pisidia longicornis (porseleinkrabbetje)
Anapagurus laevis (heremietskreeft)
Pagurus bernhardus (heremietskreeft)
Pagurus prideauxi (heremietskreeft)
Diogenes pugilator (heremietskreeft)
Ebalia tumefacta (gladde kiezelkrab)
Inachus dorsettensis (gestekelde sponspootkrab)
Achaeus cranchii (wratoogkrab)
Macropodia rostrata (gewone hooiwagenkrab)
Hyas coarctatus (rode spinkrab)
Hyas araneus (gewone spinkrab)
Eurynome aspersa (paddestoelkrab)
Thia scutellata (nagelkrab)
Corystes cassivelaunus (helmkrab)
Cancer pagurus (noordzeekrab)
Portunus latipes (breedpootkrab)
Carcinus maenas (strandkrab)
Liocarcinus holsatus (gewone zwemkrab)
Liocarcinus marmoreus (gemarmerde zwemkrab)
Liocarcinus depurator (blauwpootzwemkrab)
Liocarcinus arcuatus (gewimperde zeekrab)

Necora puber (fluwelen zwemkrab)
Pilumnus hirtellus (harig krabbetje)
Pinnotheres pisum (erwtkrabbetje)

ECHINODERMATA (stekelhuidigen)

Asterias rubens (zeester)
Ophiura ophiura (brokkelster)
Ophiura albida (brokkelster)
Ophiura affinis (brokkelster)
Ophiura sp.
Amphiura filiformis (slangster)
Amphiura brachiata (slangster)
Ophiotrix fragilis (slangster)
Psammechinus miliaris (zeeappel)
Spatangus purpureus (paarse zeeklit)
Echinocardium cordatum (zeeklit)
Echinocyamus pusillus (zeeboontje)

CHORDATA

Amphioxus lanceolatus (lancetvisje)

PISCES (vissen)

Lamptera fluviatilis (rivierprik)
Galeorhinus galeus (ruwe haai)
Mustelus mustelus (gladde haai)
Scyliorhinus canicula (hondshaai)
Raja clavata (stekelrog)
Dasyatis pastinaca (pijlstaartrog)
Anguilla anguilla (paling)
Clupea harengus (haring)
Sprattus sprattus (sprot)
Alosa alosa (elft)
Alosa fallax (fint)
Engraulis encrasicolus (ansjovis)
Salmo trutta (forel)
Osmerus eperlanus (spiering)
Gadus morhua (kabeljauw)
Merlangius merlangus (wijting)
Trisopterus luscus (steenbolk)
Trisopterus minutus (kleine steenbolk)
Pollachius pollachius (pollak)
Micromesistius poutassou (blauwe wijting)
Enchelyopus cimbrius (vierdradige meun)
Ciliata mustela (vijfdradige meun)
Merluccius merluccius (heek)
Lophius piscatorius (zeeduivel - staartvis)
Belone belone (geep)
Atherina presbyter (koornaarvis)
Zeus faber (zonnevis)
Gasterosteus aculeatus (driedoornige stekelbaars)
Syngnathus rostellatus (kleine zeenaald)
Syngnathus acus (grote zeenaald)
Trigla lucerna (rode poon)
Eutrigla gurnardus (grauwe poon)
Myoxocephalus scorpius (zeedonderpad)
Enophrys bubalis (groene zeedonderpad)
Agonus cataphractus (harnasmanetje)
Cyclopterus lumpus (snotolt)
Liparis liparis (slakdolf)
Dicentrarchus labrax (zeebaars)
Trachurus trachurus (hormakreel)
Spondylusoma cantharus (zeekarper)

Mullus surmuletus (mul - koning van de poon)
Chelon labrosus (diklipharder)
Zoarcres viviparus (putaal)
Pholis gunellus (botervis)
Echiichthys vipera (kleine pieterman)
Ammodytes tobianus (zandspiering)
Gymnammodytes semisquamatus (zandspiering)
Hyperoplus lanceolatus (smelt)
Callionymus lyra (pitvis)
Callionymus reticulatus (rasterpitvis)
Pomatoschistus microps (brakwatergrondel)
Pomatoschistus minutus (dikkopje)
Pomatoschistus lozanoi (lozano's grondel)
Pomatoschistus pictus (kleurige grondel)
Aphia minuta (glasgrondel)
Scomber scombrus (makreel)
Arnoglossus laterna (schurftvis)
Scophthalmus maximus (tarbot)
Scophthalmus rhombus (griet)
Pleuronectes platessa (schol - pladijs)
Pleuronectes flesus (bot)
Limanda limanda (schar)
Microstomus kitt (tongschar)
Solea solea (tong)
Buglossidium luteum (dwergtong)

AVIFAUNA (zeevogels)

Gavia stellata (roodkeelduiker)
Gavia arctica (parelduiker)
Gavia immer (ijsduiker)
Podiceps cristatus (fuut)
Podiceps griseigena (roodhalsfuut)
Podiceps nigricollis (geoorde fuut)
Fulmarus glacialis (noordse stormvogel)
Puffinus gravis (grote pijlstormvogel)
Puffinus griseus (grauwe pijlstormvogel)
Puffinus puffinus (noordse pijlstormvogel)
Hydrobates pelagicus (stormvogeltje)
Oceanodroma leucorhoa (vaal stormvogeltje)
Morus bassanus (jan van gent)
Phalacrocorax carbo (aalscholver)
Phalacrocorax aristotelis (kuifaalscholver)
Somateria mollissima (eidereend)
Melanitta nigra (zwarte zee-eend)
Melanitta fusca (grote zee-eend)
Phalaropus lobatus (grauwe franjepoot)
Stercorarius pomarinus (middelste jager)
Stercorarius parasiticus (kleine jager)
Stercorarius longicaudus (kleinste jager)
Stercorarius skua (grote jager)
Larus melanocephalus (zwartkopmeeuw)
Larus minutus (dwergmeeuw)
Larus sabini (vorkstaartmeeuw)
Larus ridibundus (kokmeeuw)

Larus delawarensis (ringsnavelmeeuw)
Larus canus (stormmeeuw)
Larus fuscus fuscus (kleine mantelmeeuw)
Larus fuscus graellsii (kleine mantelmeeuw)
Larus argentatus (zilverbmeeuw)
Larus cachinnans (geelpootmeeuw)
Larus marinus (grote mantelmeeuw)
Larus hyperboreus (grote burge-meester)
Rissa tridactyla (drieteenmeeuw)
Gelochelidon nilotica (lachstern)
Sterna sandvicensis (grote stern)
Sterna hirundo (visdief)
Sterna paradisaea (noordse stern)
Sterna albifrons (dwergstern)
Chlidonias niger (zwarte stern)
Uria aalge (zeekoet)
Alca torda (alk)
Alle alle (kleine alk)
Fratercula arctica (papegaaieduiker)

MAMMALIA (zeezoogdieren)

Lagenorhynchus albirostris (witsnuitdolfijn)
Lagenorhynchus acutus (witzijdedolfijn)
Phocoena phocoena (bruinvis)
Halichoerus grypus (grijze zeehond)
Phoca vitulina (gewone zeehond)



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